TEXT-BOOKS OF ANIMAL BIOLOGY

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LIFE IN INLAND WATERS

WITH ESPECIAL REFERENCE TO ANIMALS

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Edited by JULIAN S. HUXLEY

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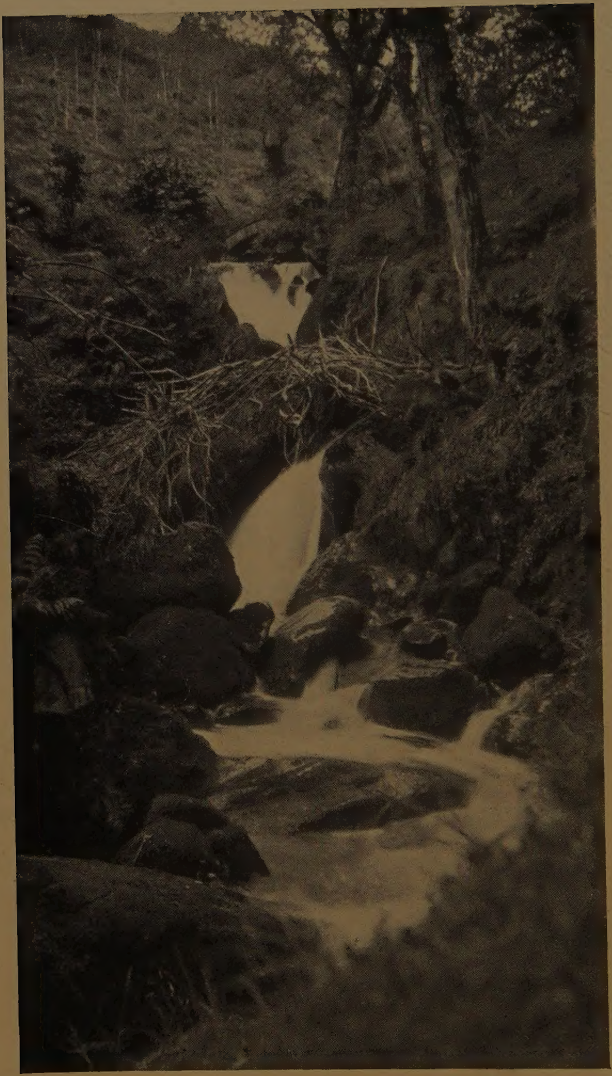
PLATE I



The cascade-reach of a Welsh highland brook.

Frontispiece.]

LIFE IN INLAND WATERS

WITH ESPECIAL REFERENCE TO ANIMALS

BY

KATHLEEN E. CARPENTER

WITH AN INTRODUCTION BY

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TO

MY FATHER

AUTHOR'S PREFACE

THE life of inland waters—to its student, the phrase recalls pictures vignetted against a background of wooded hills and open sky, of pools tree-fringed or rock-encircled, of clear brooks cascading from sunlit reach to quiet pool, or of slow rivers streaming through the level flats, where willows stoop above them. Pictures of the trout, seen dimly where he lurks, head turned upstream, beneath the hollow bank, or splashes up to seize his living prey; of darting minnows, arrowy shapes across the clear sands of the brook; of the great beetle, diving in his silvery coat of air-entangling mail; of the mayfly nymph that spreads her grapnel limbs beneath the sheltering stone, clinging against the swift current that bathes her tufted gills, or of that mayfly cousin that digs entrenchments in the sandy bank; of caddis-worms that trail their cylinders of leaf-mosaic, with spreading trains of twigs, across the muddy floor, or—spiders of the rapids—spread silken snares full in the path of the rushing stream; of all the myriad, fragile forms that shelter in the crannies of the pebbles, that crawl upon the mud, or lie half-buried in the soft ooze below; of those yet more delicate and lovely creatures, just visible to the unassisted eye, that drift or swim free in the calm waters; of pond-skaters, those pirates of the pool, whose beaked galleys dart upon the surface-film—pictures of all these, and a thousand more, the phrase brings back to those who know and love the world of the fresh waters.

It is a world of infinite beauty, infinite variety, infinite charm; a world, too, which lies freely open for our exploration, and yet how many, even of professed biologists, have penetrated beyond its threshold? The numbers are all too

few, though led by pioneers like Rêaumur, Lyonnet, and Swammerdam, for some of whom the fascination of that adventure outweighed all other claims.

The charm and freshness of the early studies in natural history, which might well be called " biology " (a title often misapplied to-day), dissolving before the thunders of the Darwinian controversy, gave place throughout the field of natural science, and of zoology in particular, to minute study of the anatomy of dead material, supplemented by embryological detail ; for a time the true conception of biology as the study of the living being seemed in danger of oblivion, but the wheel has turned again. Recent advances in bio-chemistry, in combination with an entirely new appreciation of the true scientific basis of economic biology, have stimulated an interest in the conditions of tenure of life in situations of different types, and the young science of Ecology begins to take firm stand upon foundations laid by an earlier generation of biologists.

The life of the ocean, with its infinite fertility and variety of type, has always offered irresistible attractions and opportunities to anatomist, embryologist, and physiologist alike, and in these sea-girt isles of Britain its problems, never far to seek, have in large measure engrossed the energies even of followers of the new tradition in Hydrobiology. Further, a charge of monotony and paucity of type has been brought against that neglected world of the fresh waters which for most of us lies even closer at our doors ; but students of other races have discovered its problems to be no less manifold, no less engrossing than those of the sea. In America, with its great sheets of inland water, in Central and Northern Europe, with their many lesser lakes and network of rivers flowing by long courses to a far-off sea, marine conditions are less readily accessible, and the problems of the fresh waters more intimate and more pressing through the importance of inland fisheries in the national economy. In recent years the science of freshwater biology has progressed by great strides in these countries of the European mainland and America, while we in Britain have but little to contribute. Among our scanty

enterprises, that of the survey of Scottish inland lochs, conceived and directed by Sir John Murray, looms large; but even this was inspired by the example of studies, already far advanced in Europe, which had yielded results of far-reaching consequence, to which this British work could only form a belated, yet a valuable appendix. But this enterprise, so well sponsored and so full of promise, was destined to remain incomplete, and seriously so on its biological side; a few recent separate studies of lake-fauna must receive mention in our later pages, but with all the varied problems of the life of rivers, springs, limestone-caverns, and of pools of different types, whose knowledge on the Continent is fast being brought to maturity, British biology in general has had little concern. True, a few scattered studies, undertaken in recent years, encourage a belief that the flame is kindled, but it flickers feebly yet, and may die unless an interest in this field, so fertile of opportunity, can be stimulated. Such stimulus can best be given through the medium of the Universities, whose students will contribute either to the deepening of knowledge or to its dissemination, and the interest of students in a topic hitherto unfamiliar must be aroused by the presentation of a general survey of the subject and its problems without laying too great stress on technical minutiæ.

Several general works on Freshwater Biology have been published in Germany and in America; while each has its own very special value, not one seems calculated to serve exactly the purpose indicated. It is the pressing need of a compilation suitable for use by British students which has encouraged the writer to undertake a task whose difficulties and responsibilities might well deter more competent and experienced biologists than one whose only claim to fitness for it rests upon an enthusiasm which will not be denied.

The standpoint of the work is ecological throughout: no attempt is made to deal with "systematics" or method. There is no royal road to identification of species, nor is it possible to construct a key to British freshwater species, so many insect-larvæ being as yet undescribed: Brauer's *Süsswasserfauna Deutschlands*, supplemented by monographs on

the separate groups, will be a valuable guide, while, in the matter of method, the student cannot do better than consult the appropriate sections of Abderhalden's *Handbuch der Arbeitsmethoden*, and the useful hints on collection and preservation of specimens in Ward and Whipple's *Freshwater Biology*.

Only the pleasant duty of giving thanks remains: and here I wish to set on record my deep indebtedness to all those friends whose sympathy and encouragement have led me to the completion of this work—especially to Professor D'Arcy Thompson. My sincerest thanks are due to Professor R. Douglas Laurie for facilities regarding literature, also to Mr. B. Storrow for the opportunity to read new work in proof, and to the Council of the Royal Society of Edinburgh for kind permission to reproduce some of the photographs from Mr. G. West's *Flora of the Scottish Lakes*. Acknowledgments of another kind are due to the Department of Scientific and Industrial Research, under whose auspices was carried out the original work which led me to a wider interest in Freshwater Biology. Finally, I must express my appreciation of the kindness of the editor of this series.

KATHLEEN E. CARPENTER.

LONDON.
April, 1928.

EDITOR'S INTRODUCTION

Good wine needs no bush, and Dr. Carpenter's book has no need of commendatory prefaces. I would, however, like to emphasize one point in relation to the general plan of this series of books. They aim at providing introductions to different branches of biological science, which may rightly find a place in the undergraduate training of students. Freshwater biology has been much neglected in the past. Her Cinderella charms have been eclipsed by those of her elder and more ample sister, Marine Biology. It is perfectly true that the variety and fullness of animal life can never be properly appreciated without visiting the sea-coast; none the less, freshwater biology may be destined to play an important rôle in the educational scheme. Even in a little island like our own, it is not every student who can manage a visit to a marine laboratory. But fresh water is everywhere; and in streams and ponds and freshwater aquaria a great many important biological problems can be thoroughly and practically studied. The facts and principles of what may be called physiological natural history find, perhaps, their readiest demonstration in the life of inland waters.

The adaptation of form to function and the development of special modes of reproduction and special physiological characters in relation to the characters of the environment are beautifully illustrated by freshwater animals, according as they inhabit swift brooks or sluggish rivers, clear springs or stagnant ponds, large lakes or the trivial films of moisture within the soil or in damp mossy spots. Freshwater habitats are extremely varied; and the methods for determining and measuring those of their physical and chemical characteristics

which influence the life which they harbour are well developed and relatively easy to carry out. On all these points Dr. Carpenter's book provides a rich store of facts, well chosen to illustrate the general principles of the subject.

It is true, as Dr. Carpenter further demonstrates in her book, that freshwater animals also provide us with excellent material for studying various problems of migration and evolution, of ecology in its strict sense of the natural history of communities, of geographical distribution, and of economic zoology. But I venture to think that from the point of view of the teacher and of the average student in the average undergraduate course in zoology, the prime importance of the subject will lie, as I have said, in its providing easily accessible material and vivid illustrations of the adjustment of organism to environment. The material lends itself readily both to observational and experimental study, and illustrates both the physiological adjustment of the individual and the evolutionary adjustment of the race. It ought to be the teacher's main standby in bringing his students to real grips with the problem of adaptation, not in any academic or armchair fashion, but practically and directly.

Dr. Carpenter, in her book, reveals yet another motive for the study of freshwater biology—the love of nature for its own sake. To be able to indulge that love oneself and to foster it in others will appeal to many teachers who may feel that the ordinary zoological curriculum is unduly arid, and that its dry bones should be clothed with living flesh. To them this book should have a double appeal. And the feeling which underlies it, and the skilfully chosen array of quotations from Izaak Walton which head its chapters should be a reminder of the great part which the amateur (in the true sense of that word) has played in advancing biological knowledge and biological thought, and the vitalizing effect on academic theory and laboratory practice of that return to the open air to which the love of nature compels her true votaries.

JULIAN S. HUXLEY.

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LIFE IN INLAND WATERS

CHAPTER I

THE ORIGIN AND GENERAL CHARACTERISTICS OF THE FRESHWATER FAUNA

"And an ingenious Spaniard says, that rivers and the inhabitants of the watery element were made for wise men to contemplate, and fools to pass by without consideration, . . . for you may note, that the waters are Nature's storehouse, in which she locks up her wonders."—IZAAK WALTON.

BIOLOGY, in the strict meaning of the word, is the study of life itself—an inquiry into its origin, its history, and the secret of its maintenance upon the earth. An aim so abstract must needs be approached through concrete instances, and so for most of us the foundation of our biology is laid by study of the form and structure of as many individual types of living beings as possible, of the essential functions of their various organs, and of their differences from one another. But when our knowledge of morphology, physiology, and systematics is well established, the real task of biological studies has yet to be commenced, and we must now try to appreciate the way in which these several types maintain their own existence, and that of their races, in relation to the world in which they find themselves. Life is dynamic: it is neither a free gift nor a prize, once won and held thereafter without effort, but rather a continual commercial enterprise, a bargaining between the organism and its environment. For every moment's life we pay the price—our pound of flesh—out of the very stuff of life itself, burning away our substance to maintain the vital spark: we lose our life to save it. This loss must be made

good, in the last instance, by drawing on the stores of inorganic matter: it follows, therefore, that for the comprehension of that life with which biology concerns itself we must appreciate the outer circumstances which form its setting.

Some artists tell us that in order to appreciate a landscape one should stand upon one's head, or in some other way contrive to see it upside down: familiar details gain a fresh significance from the new viewpoint. In the same way, to a biologist trained in the school of anatomy, and used to thinking first of the type, then of its circumstances, the opposite line of approach may bring new comprehension, though at first, perhaps, it may induce a little giddiness. It is our aim throughout this study of the life of inland waters first to appreciate the conditions under which that life is held, then to discover how these conditions have been turned to best advantage by living beings. A fundamental knowledge of the groundwork of morphology, physiology, and classification will therefore be assumed, and these will serve as handmaids to our study of the whole.

Phylogenists maintain that the origin of life was in the waters, basing their argument upon the presence of so many types of primitive structure, representing all the simplest tribes of the great phyla, in the aquatic medium. From our new standpoint it is appropriate to consider how far this habitat, as compared with the terrestrial, may appear suitable for the origin and maintenance of life. The living substance, which we call protoplasm, is a mixture of complex compounds known as proteins (containing the elements carbon, hydrogen, oxygen, nitrogen, phosphorus, sulphur), into whose composition water enters largely, and as antecedent to its formation demands the building up of nitrogenous substances for whose first origin we must postulate the intervention of some powerful electrical or other physical disturbance. The theory first advanced by Osborn [1] of the influence of electrical disturbances, such as still take place, on a smaller scale, in thunderstorms, as well as the stress laid by Macfarlane [2] on the complex chemical reactions which occur in shallow pools near centres of volcanic

[1] For this and similar references see end of the chapter.

activity, alike suggest that life may well have been evolved in small and shallow water-bodies where such influences would be strongly felt, rather than in the larger masses of the ocean. It is true that we know little of the composition of the primal ocean, beyond the fact that its salinity has steadily increased throughout the ages by contributions of inorganic salts brought down by the rivers [3]; but certainly before it could become fertile of life it must have been enriched by the addition of nitrogenous compounds such as are now supplied ultimately by the agency of the nitrogen-fixing bacteria. Some creatures comparable in their mode of life to the modern *Nitrosomonas* and *Nitrobacter* were probably the first to be evolved: later, in water now enriched with nitrates, the first true autotrophic organisms of flagellate type would accede, to be followed again by holozoic forms which preyed upon them. If these phases occurred in shallow pools, we might expect to find in inland waters some representative survivors of the primitive forms of life, and this is actually the case. The nitrogen-fixing bacteria, though by no means confined to the fresh waters, are very numerous there, as in the soil and sea, and of the Protozoa all the simplest types are to be met with here. Euflagellata, which are held by many biologists to be the most primitive of all, are specially characteristic of fresh waters; simple amœboid forms and shelled Lobosa are common to these and to the seas, and some species are even tolerant of both media; among Foraminifera, only the most primitive order, the Allogromidaceæ, belong to the fresh waters, while all higher types are marine; although the Infusoria are perhaps more numerous in the fresh waters than in the seas, by contrast some of the groups of highest complexity of structure among the Protozoa (Radiolaria, Choanoflagellata, Dinoflagellata, Cystoflagellata) are all characteristically marine. The facts appear to indicate at least a very early penetration of fresh waters by the Protozoa, before the subclasses had been differentiated, and may be even held for evidence of a freshwater origin for the whole phylum. Our modern freshwater Flagellates and Rhizopods may be the relics of an ancient stock, evolved at a very early period in the

world's history, and still surviving, though doubtless somewhat modified, in the terrestrial waters from which they have sent out pioneers for the colonisation of the oceans.

Life in the waters, whether they be salt or fresh, undoubtedly presents many advantages over its counterpart on land, especially to living beings of small size and simple structure. In that vital commerce by which the organism maintains existence, the capital stock is protoplasm, in which water bulks largely, while the chief medium of exchange and transport is water itself: the greatest danger, then, to which a living being can be exposed is that of desiccation. Terrestrial animals and plants alike have means to guard against this constant peril: those moist and permeable membranes through which alone the vital interchange of gases can take place are localised in well-protected areas—as the lungs of Vertebrates, tracheæ of insects, air-spaces of flowering plants—while the general surface is covered by a drought-resistant membrane, a hairy or a scaly coat. All such devices entail first, complexity of structure, next, great expenditure of energy and material to maintain the special organs: remove the fear of desiccation, and it becomes possible to save much of this expense and to maintain life on a simpler basis.

A second danger, scarcely less severe, lies in exposure to extremes of temperature. Great heat is fatal to the living substance, and heat of less degree, if long endured, may lead to desiccation, while external cold may rob the organism of that precious energy which is the object of its vital commerce. To guard against such dangerous extremes, animals of terrestrial habit must exhibit modifications, structural and physiological, which again entail expenditure of material and the evolution of a complex form.

From both these perils the aquatic habit gives at least comparative security: danger of desiccation is reduced to a catastrophic possibility, in place of a constant menace, while even quite small bodies of water have a high degree of thermal conservatism, due to the very great specific heat of water.

The density of water is also high—over 700 times that of air at normal atmospheric pressure: this, and the allied

property of viscosity, which increases more rapidly than the density in passing to low temperatures, combine to reduce the effective sinking-weight of submerged or floating bodies. The problem of locomotion for aquatic animals is thus simplified by lessening the pull of gravity and relieving the necessity for large, weighty, and biologically expensive skeletal supports, and these properties of the aquatic medium, by reducing the force of mechanical shocks, reduce also the need for strong protective integuments: again, the balance, as compared with terrestrial conditions, is in favour of the survival of small and simple organisms. Further, the solvent properties of water and its powers of convection maintain a constant free supply of dissolved gases and salts in all but abyssal depths, while currents, bearing suspended matter which includes organic particles of high food value, encourage the development of vast numbers of those small microphagous or current-feeding types which are peculiar to the aquatic medium and which represent so many divergent lines of animal descent.

It is little wonder, then, that many small and lowly organisms are confined to the aquatic habitat, and that life itself is considered to have originated in this medium, which presents so many characteristics favourable to its development and easy maintenance.

The fauna of the inland waters (lakes, rivers, and other continental water-bodies, mainly though not exclusively "fresh") is generally credited with a certain monotony and paucity of types, which, by contrast with the infinite variety and abundance of life in the sea, has discouraged many biologists from giving it their close attention. These features are held by students of freshwater biology to be more apparent than real, yet it is appropriate to compare the general constitution of the freshwater fauna with that of the marine, and for this purpose a tabular arrangement may be adopted.

Phylum.	Class.	Sub-class.
I. Protozoa	A. Rhizopoda.	1. Lobosa.
		2. Foraminifera.
		3. Heliozoa.
		4. Radiolaria.
	[B. Mycetozoa—exclusively terrestrial.]	
	C. Mastigophora.	1. Euflagellata.
		2. Choanoflagellata
		3. Dinoflagellata
		4. Cystoflagellata
	[D. Sporozoa—exclusively parasitic.]	
	E. Infusoria.	1. Ciliata
		2. Tentaculifera
II. Porifera	A. Calcarea	
	B. Hexactinellida	
	C. Demospongia.	
III. Cœlenterata	A. Hydrozoa.	
	B. Scyphozoa	
	C. Actinozoa	
	D. Ctenophora	
IV. Platyhelminthes ..	A. Turbellaria.	1. Polycladida.
		2. Tricladida.
		3. Rhabdocœlida.
	[B. Trematoda	
	C. Cestoda Parasitic.]	
V. Nemertinea		
VI. Nematoda		
VII. Trochelminthes. ..	A. Rotifera.	
	B. Gastrotricha.	
VIII. Echinodermata ..		
IX. Brachiopoda ..		
X. Polyzoa	A. Endoprocta.	
	B. Ectoprocta.	
XI. Annelida	A. Archi-Annelida.	
	B. Chætopoda.	1. Polychæta.
		2. Oligochæta.
		3. Hirudinea.
	C. Gephyræa.	

Representation	
In the Sea.	In Fresh Waters.
Marine and fresh water.	
Mainly marine.	Only Allogromidaceæ (the most primitive order) in fresh water.
(Very few marine species.)	Mainly fresh water.
All marine.	
	Practically all fresh water.
Almost entirely marine.	Three genera in fresh water.
Occur in both media: more numerous in fresh water.	
Exclusively marine.	
Essentially marine.	A very few species in fresh water.
Mainly marine.	*Hydra* and a very few Hydromedusæ in fresh water.
All essentially marine.	
All marine.	
A few marine.	Mainly fresh water.
Marine, fresh water, and terrestrial.	
Essentially marine.	One or two species in fresh water.
Common to sea, fresh water, and soil.	[Many parasitic.]
Very few marine.	Essentially fresh water.
	Exclusively fresh water.
Exclusively marine.	
Exclusively marine.	
Exclusively marine.	
Mainly marine.	One specialised order (Phylactolæmata) and a single other genus (*Paludicella*) in fresh water.
Exclusively marine.	
Essentially marine.	One or two species in fresh water.
Very few marine species.	Essentially fresh water or terrestrial.
Common to sea, fresh water, and land.	
Exclusively marine.	

Phylum.	Class.	Sub-class.
XII. Arthropoda ..	.. A. Crustacea.	1. Branchiopoda. 2. Ostracoda. 3. Copepoda. 4. Cirripedia. 5. Malacostraca.
		[The extinct primitive Trilobita
	B. Prototracheata Myriapoda Insecta	All essentially sub-aerial, throughout life. Only
	C. Arachnida.	Essentially sub-aerial, Hydrachnidæ).
XIII. Mollusca. ..	.. A. Gastropoda.	1. Amphineura. 2. Streptoneura. 3. Euthyneura. Orders : *a*. Opistho-branchiata. *b*. Pulmonata.
	B. Lamellibranchia.	
	C. Scaphopoda D. Cephalopoda	
XIV. Congeries of Sub-Phyla	Hemichorda Cephalochorda Urochorda	
XV. Vertebrata (Craniata).	A. Cyclostomata.	
	B. Pisces.	1. Elasmobranchii 2. Holocephali
	Archaic tribes with only a few surviving species.	3. Dipnoi. 4. Crossopterygii. 5. Chondrostei. 6. Holostei.
		7. Teleostei.
	C. Amphibia.	
	D. Reptilia E. Mammalia F. Aves	All essentially sub-aerial : fresh water, though are secondarily marine.

Representation: In the Sea.	Representation: In Fresh Waters.
Very few marine species.	Essentially fresh water.
Mostly marine.	Some freshwater forms.
Marine and fresh water.	
Exclusively marine.	
Chiefly marine.	Scattered genera, and even species of marine genera, in fresh water.
were a marine tribe.]	
but many Insects have freshwater larvæ, and a few remain aquatic very few are associated with marine waters.	
but include one marine and one freshwater family of Mites (Halacaridæ	
Exclusively marine.	
Essentially marine.	Some freshwater genera, of several families.
Essentially marine.	
	Terrestrial and fresh water.
Mostly marine.	A number of freshwater types, mostly of Unionidæ.
Exclusively marine.	
All exclusively marine.	
Fundamentally marine—some penetration up rivers.	
Exclusively marine.	
	Fluviatile.
	Fluviatile.
Marine and fluviatile.	
	Fluviatile and lacustrine.
The majority are marine.	Cyprinidæ are entirely fresh water, also certain members of a number of other families.
	All fresh water or terrestrial.
a few are secondarily adapted for a semi-aquatic existence, usually in three or four orders of fossil reptiles and a few existing birds and mammals	

The case of Protozoa has already been considered, but, when we turn to other phyla, we cannot fail to note that these in general are less abundantly represented in fresh waters than in the sea: Echinoderms and Brachiopoda, as well as the mixed assemblage of primitive or degraded forms near the base of the Chordate series, are entirely lacking, while the majority of Porifera and Nemertines, the Cephalopoda and the Gephyræa are exclusively marine. Further, within each group the distribution is usually reversed from the type which we found to characterise the Protozoa: the main body of the group is generally marine, with either one or two specialised orders in the fresh waters (*e.g.* Phylactolæmata and Cyprinidæ), or else scattered families, genera, or even species whose nearest affinities are with marine stocks. This condition is the strongest evidence that the main mass of the fauna of fresh waters is not homogeneous and indigenous in origin, but owes its character to their invasion by representatives of a variety of stocks already differentiated elsewhere, and probably first established in the pelagic region of the ocean, where the uniform conditions encouraged rapid development of life [4]; on the whole, the fauna of the inland waters is an *immigration fauna*.

FIG. 1.—Portion of a colony of *Cordylophora lacustris* (after Simroth).

Such immigration is by no means at an end, for we have records of instances within the memory of man. The most familiar case is that of the Anthomedusan *Cordylophora lacustris*, early known as a denizen of salt or brackish water, which in 1854 established itself for the first time in canal-docks in Dublin and in Belgian rivers, and was later traced up the Seine and some German and East Anglian rivers [5]: it was doubtless carried up by passive transport, as it has the habit of fixing itself to ship-bottoms or floating wood, and it has proved able to establish itself in the new surroundings.

Few other instances of recent penetration by marine types are so definitely established, and *Dreissensia polymorpha*, the zebra-mussel, is perhaps the only other whose invasion can be even approximately dated: this species appeared in the Volga and the Danube during the eighteenth century, and about a century later was found to have invaded a number of rivers in Western Europe.[6] In Britain, the Gastropod Mollusc, *Paludestrina jenkinsi*, an estuarine and brackish water form, seems to have recently penetrated to quite fresh waters near certain coasts.[9] A number of other cases of the occurrence of marine species in inland waters are well authenticated, although the date of their establishment is not known: shore-living species of *Zoarces* and *Blennius*, fishes of the rock-pools, not infrequently come up the rivers, and the flounder (*Platessa flesus*) is known to wander for long distances up the Weser and Rhine, as far as Metz on the Moselle River [6, 7]; a species of *Nereis* has been found in a lake of fresh water,[8] and several Indian rivers include representatives of Molluscan genera believed to be marine (*Scaphula*, *Teredo*, . . .).[5, 7, 8]

FIG. 2. — The zebra-mussel (*Dreissensia polymorpha*). *f*, foot; *b*, byssus; *e*, *i*, exhalent and inhalent siphons (after Woodward).

The question may well be asked, why is such penetration not more general? Rivers are in open communication with the sea, and both media have certain fundamental features in common: identical organs of locomotion and respiration would presumably serve the needs of animals in either medium, while the change might appear to offer no very serious impediment to the other vital functions of nutrition and excretion. True, the constant streaming of a seaward current and the frequent presence of a muddy intertidal zone near the mouth of a river may constitute an obstacle to weak swimmers and soft-bodied animals in particular, but a delicate type like *Cordylophora* has been able to survive the passage, and tidal

action must tend to increase the chances of stranding above the turbid zone, while many littoral fishes and Crustacea are quite able to hold their own and even to make headway against a current of some force. The true obstacle to immigration is no physical barrier, but a change in the chemical constitution of the aqueous medium which is responsible for the death of marine animals on entering fresh water.

It is common experience, authenticated by a number of experimenters,[8, 10, 11] that sudden immersion in fresh water is fatal to representative marine animals, and *vice versâ*, and experiment is confirmed by the observation that the majority of aquatic species are confined strictly throughout life to one or the other medium. Only a few exceptional types, such as the flounder, the common stickleback, salmon, and eels, are known to pass unharmed between the two, whose superficial resemblance masks an essential difference in chemical content of far-reaching biological consequences. This difference is illustrated by the following table of solution-content of water from the North Atlantic Ocean and from the River Thames, quoted from Sollas.[3]

Dissolved material (in parts per 1000).	North Atlantic water.	Thames water.
Calcium Carbonate	0·04	0·168
Magnesium Carbonate	—	0·018
Calcium Sulphate	1·40	0·044
Magnesium Sulphate	2·21	—
Potassium Sulphate	—	0·002
Sodium Chloride	27·73	0·016
Magnesium Chloride	3·44	—
Potassium Chloride	0·68	0·009
Silica	0·015	0·009
Organic matter, etc.	—	0·035
	35·52	0·301

The total solution content of inorganic salts (commonly called "salinity") is seen to be over 100 times as great in a representative portion of the ocean as in the river, the excess being largely due to the presence of common salt.

A large-scale example of the relations of an aquatic fauna

to the salinity of the medium is seen in the case of the Baltic Sea, the water of whose eastern and northern reaches, owing to the supply brought in by rivers in excess of the slow evaporation in a cool climate, has a lower salinity than that of the western portion, which communicates directly with the open sea. The Molluscan fauna of the Baltic, in particular, exhibits a marked gradation and diminution of species from west to east, the more sensitive types, such as *Tellina*, disappearing as the salinity is reduced.[7] Scyphozoan Medusæ, ocean-born, drift in on currents through the Kattegat and are commonly found far into the Baltic; reproduction may take place freely as far as the planula and scyphistoma stages, but strobilation has never been observed in the zone of low salinity, and the supply of individuals is renewed only from the outside.[12] Certain animals found living in the deeper waters of the Kattegat and Great Belt die speedily when raised to the surface stratum, a mortality which is attributed by Semper [7] to the change in salinity rather than to alterations in temperature, which apparently are not considerable in this case.

Botazzi [13] has shown that the internal fluids (blood serum, cœlomic fluid, etc.) of a number of marine Invertebrate animals representing widely separated natural groups have an osmotic pressure (as measured by the depression of the freezing-point) which approximates very closely to that of their native element, and that the same is true for Elasmobranch fishes; in many freshwater species the osmotic pressure is a good deal lower, though still distinctly above that of the water in which they live.[13, 14] Macallum, on the basis of similar observations, propounded the theory that the saline constitution of the body-fluids of a species reflects that of the medium in which the species originated,[15] and although the theory must not be carried to extremes, the relationship is striking in the case of marine Invertebrates at least. Liquid bodies separated by a permeable membrane tend to arrive at equilibrium in their solution content, and the presence of a membrane of this character over the respiratory surfaces of aquatic animals must encourage the establishment of such

osmotic equilibrium between the internal fluids and the external medium: the *rapprochement* may be expected to be the more intimate where the respiratory surface is not rigidly localised (as in gill-breathers), but spread over a large proportion of the body, as in many small and lowly organisms of water.

The consequences of osmotic exchange may well be fatal to aquatic animals which find their way into a medium of unaccustomed degree of salinity: raising the salinity may be expected to cause the abstraction of water from the body by exosmosis, while lowering it may lead to imbibition which causes severe functional and even anatomical strain. Such consequences actually do ensue under experimental conditions: the marine form of *Amœba crystalligera* rapidly absorbs water of relatively low salinity, and marked vacuoles appear in its cytoplasm[16]; * the bodies of marine Turbellarians placed in fresh water swell rapidly, while those of river species shrivel and curl in sea water, both processes alike ending in death; marine Capitellidæ, placed in fresh water, undergo a similar process, with the additional feature that some of the red colouring-matter of the blood oozes into the surrounding water[17]; frogs and many other freshwater animals, placed in sea water, rapidly lose weight and shrivel, indeed, in the picturesque phrase of Paul Bert,[18] "on peut drainer et tuer une grenouille en plongeant simplement une de ses pattes dans l'eau de mer." Such instances serve to convince us of the dangers and difficulties involved in entering a new aquatic medium, especially for animals in which diffusion takes place freely over a large area of the body.

Were diffusion uncontrolled, we should expect to find in wandering species a change in the constitution of the fluid roughly corresponding with the changes in salinity encountered: Dakin,[19] following fishes from Kiel Haven out

* A few Protozoan species have both marine and freshwater varieties: the case of *Actinophrys sol*, whose freshwater form is characterised by the highly foamy and vacuolated structure of its cytoplasm, as compared with the greater compactness of the marine, must surely be interpreted in the light of experiments just noted as indicative of a close relation between osmotic pressure in the medium and structural modifications in the organism.

over the North Sea, found that there was correspondence to a certain, but limited, extent, and that the degree of correspondence varied with the species. Evidently there is some control of osmotic exchange, which Dakin suggests may be engineered by the regulation of kidney-secretion in addition to a selective permeability on the part of the gill-membranes of fishes. The correspondence was slightest in the case of eels, which can and do pass in the natural course of the life-history through very varied saline media, and in their case there is no doubt that permeability is limited by the coating of mucus over gills and skin, since Bert observes [18] that a sudden change of medium becomes fatal to eels if a considerable proportion of this mucus be first brushed away. In other cases, the presence of chitinised membranes is no doubt important in retarding and limiting diffusion.[20]

The classic experiments of Beudant [10] have revealed the possibility of adjustment to changed conditions of salinity on the part of a great variety of types, provided the change be gradual. A number of animals, representing species to which a sudden change was proved to be fatal, were successfully induced to survive a change from sea to fresh water (and *vice versâ* in the case of freshwater species) which extended, by very gradual dilution, over a period of six months. At the end of this time, a number of marine animals were living uninjured in fresh water, a number of freshwater types in sea water. The percentage of survivals among the marine forms was particularly high in *Balanus striatus*, *Ostrea edulis*, and *Mytilus edulis*, particularly low in the case of *Tellina*: there is an interesting agreement between these conclusions and observations on the Baltic fauna, already mentioned.

Such facts would appear to lend strong support to the view that many freshwater forms have evolved from immigrants, functionally euryhaline (*i.e.* tolerant of widely varying conditions of salinity), probably in virtue of some physiological limitation of diffusion, which have made their way upstream along the rivers: among these, Teleostean fishes are likely to have been the most important. On the other hand, the fauna may also be recruited to no small extent from among the

littoral types of a coastal zone in which the slow freshening of stretches of salt-lagoon provided opportunities for a gradual physiological adaptation to freshwater conditions.

The increase of temperature variations met with in fresh waters has probably given added force to the chemical changes in their biological significance: this action has been demonstrated in the case of the stickleback (*Gastrosteus aculeatus*), which can survive direct transference from salt to fresh water and back, repeated on many successive days, only on the condition that the temperature be kept fairly even.[21]

The suggestion has been made that the major elements in the freshwater fauna were differentiated from marine tribes at some fairly remote period in the earth's history, when the lower salinity of ocean waters (steadily raised since then by contributions from the land) more closely approximated to those of the rivers. It is possible that a good deal of transition may have occurred in Old Red Sandstone times, as the gradual passage from marine to lacustrine conditions which occurred over wide areas in this epoch must have provided opportunities of adaptation: some of the Ostracoderm "fishes" of the Lower Old Red deposits of Perthshire are considered to be freshwater or estuarine types,[22] and a fossil bivalve allied to *Anodonta* occurs in the same series.

Von Martens [23] long ago suggested that active immigration into fresh waters had its focus in tropical regions, where the temperatures of all waters are consistently high, but modern workers lay emphasis rather on conditions of salinity, and, in striking contrast to von Martens' theory, de Guerne and Richard [24] have proposed a Polar origin for the freshwater fauna, holding that in Arctic regions (where, also, the temperatures are uniformly low, so minimising chemical effects) marine types are likely to become inured to considerable variations in salinity occasioned by alternate freezing and thawing of the water. Certainly many of our European freshwater species seem to be Nordic in origin, and the plankton in particular is richer in the colder zones, but each of these circumstances is capable of an alternative explanation (to be discussed in a succeeding chapter—V), and, although many

Arctic species are primitive within their genera, and there is some evidence of separate origin for Arctic and Antarctic stocks,[25] we find no certain examples of still continuous immigration into the fresh waters of Northern Europe near the Arctic fringe, such as might be expected on the basis of this theory. Examples of the kind are far more numerous from the coastal lands of South-East Asia and the neighbourhood of the Black Sea, and Pelseneer [26] suggests that the main avenues of penetration probably lead from the margins of warm seas of low salinity in regions of heavy monsoonal rainfall and of even temperature.

Of the making of theories there is no end: one solid rock of fact emerges, that the main mass of the freshwater fauna has undoubtedly been derived from marine types, and probably chiefly from inhabitants of the littoral zone, where euryhaline, eurythermous, and generally resistant species predominate. The failure of many forms to penetrate the fresh water may be ascribed either to their stenohaline and stenothermous character as denizens of the open seas, where equable conditions of salinity and temperature prevail, or to their passive drifting or weak swimming habit (*e.g.* Ctenophora); but one group of hardy littoral types, the Cephalopods, and many Gastropods of the intertidal zone, have notably failed as immigrants, and Sollas [27] suggests that their failure may be due to the absence of suitable and sufficient food for these greedy carnivores.

There remains a considerable element in the freshwater fauna for which a marine origin cannot be postulated, since their nearest relatives are not to be found in the seas, but on land or in the air, and of this element the Insects form the main constituent.

A large number of insect species are aquatic in habit during some portion of their lives, and the environment agrees with them so well that in many of the smaller bodies of fresh water at certain seasons they outnumber the representatives of all other tribes combined. The clouds of midges and sand-flies which rise from the shallows in early summer, the myriads of mayflies which sometimes die upon the banks in heaps, the dragon-flies which dart across the water, the caddis-flies

which hover like moths above it—all these, and more, have larval phases, often extending over several years, in which they are entirely aquatic; other insects, water-beetles, water-boatmen, and even a few Hymenoptera, are aquatic throughout life: some live submerged, and only occasionally visit the surface, while pond-skaters and many springtails dart about the water-film. Aquatic types among insects are many and varied, and almost every one is associated with the fresh water, not with the sea.

It is a principle which holds good for many animals of diverse relationships which have wandered into new surroundings that a return is made to the old habitat at breeding-time, to deposit eggs and to permit of the young developing in that environment which was the cradle of their race. Since so many insects, representing actually eight separate orders, undergo their larval stages in fresh water, must we suppose that Insecta were originally an aquatic group for whom the fresh waters have served as highway to the land? The whole mass of anatomical and physiological evidence, as well as such scanty geological data as are to hand, is directly opposed to any such theory. The Insecta are a group of high geological antiquity, early adapted for air-breathing and for flight: fossil representatives from the Coal Measures, Devonian, and even Silurian strata possess the structures characteristic of such adaptation, and one of the most fundamental features of the entire group, the possession of branching tracheal tubes which take in atmospheric air through open stigmata, can be traced even in those forms which are most completely domiciled in the fresh waters. Even such beetles and Hemiptera as remain aquatic throughout life must either come to the surface frequently to breathe the air, or renew at longer intervals the supply which they carry down by some device of hairy felting or of arching chitinous plates; the very number and variety of the devices by which aquatic larvæ of terrestrial or aerial adults maintain their oxygen supply (see Chapter II) is evidence that secondary adaptation to life in water has occurred independently from group to group, and even from species to species. The primitive aquatic origin (which *may* have been

in fresh waters) of those early Tracheate types from which the Insects sprang is lost in the mists of antiquity: among Insects themselves life in the water is undoubtedly a new affair.

Other freshwater groups of obviously terrestrial ancestry are the water-mites (Hydracarinidæ), whose minute and delicate bodies need no special respiratory devices, and the water-spiders, which fill their stationary diving-bells with air conveyed from the surface enmeshed in the downy felting of their bodies. The mites, nearly all of which are partial parasites, especially in the young stages, have probably entered the fresh waters in the train of those animals on which they prey. Some of the most ubiquitous of freshwater molluscs, including the common pond-snails and freshwater limpets (*Limnæa*, *Physa*, *Planorbis*, *Ancylus* . . .), have apparently a terrestrial origin also, since the details of anatomy place them with certainty among the Pulmonate order of the land-snails and slugs, and these aquatic types, which retain the "lung-chamber," either live at the water's edge or rise frequently to the surface to fill the lung with air. It is true that certain abyssal forms of *Limnæa*, bottom-dwellers in deep lakes below the zone of vegetation, cannot rise in this way, and seem normally to have the cavity filled with water, but such exceptions have no weight against the overwhelming mass of evidence that these types are descended from a terrestrial stock. Their case may be compared with that of beavers, otters, alligators, and water-snakes, which, fleeing from the intensities of the struggle for existence on dry land or attracted by the abundance of food-material in the fresh waters, have partially colonised an element destined from early times to receive the overflow population of land and sea alike. Simroth, in a compilation of elaborate detail, argues that the fresh waters served as high roads for colonisation of the land by types originally marine,[7] but the attractive simplicity of such a sequence vanishes when we come to consider the facts of organic relationship and also the theoretical difficulties of the conception. The evolution of terrestrial types is marked in general by the strengthening of the limb-axes for support instead of balancing or swimming, by the acquisition of a

hardened or felting integument, protective against extreme temperatures and drought as well as mechanical shocks, by modifications in the circulation and the function of the skin, by the substitution of sac-like lungs for blood-gills: for adaptations of such nature, a preliminary sojourn in fresh waters would afford but little chance of preparation. Only among the fauna of the marginal zone where air and water meet, certain terrestrial forms may have originated from the freshwater stock, but for the most part the adoption of the freshwater habit has involved the solution of problems peculiar to itself.

General Characteristics of the Freshwater Fauna.

These elements, derived from sources so diverse, may yet, in virtue of their community of circumstance, exhibit certain features which, if not common to all, at least so far predominate among them as to confer upon the freshwater fauna a recognisable general character. Such a character will inevitably be based upon modifications in physiology rather than in anatomy, yet there are evidences that the passage from waters of a high salinity has not been without effect upon structural type. The structural peculiarities of freshwater Heliozoa, as distinguished from marine, have already been mentioned, and there seems little doubt that the contractile vacuole of many freshwater Protozoa is primarily useful in discharging excess water absorbed from the surrounding medium, since in marine types the organ is generally lacking, and an increase in the salinity of the water suspends its function in freshwater *Amœbæ*.[28] The large excretory glands of freshwater Crustacea, often disproportionate in size, compared with those of marine species, probably serve the same purpose of maintaining the original constitution of the body-fluids, counteracting endosmosis, and it has recently been demonstrated that the large kidneys of Amphibia have a similar function. Such modifications are perhaps mainly physiological, but a clear example of a structural change is seen in the stickleback, *Gastrosteus aculeatus*. Although the individuals can pass unharmed

between salt and fresh water, those sticklebacks which live in the latter medium differ so much in external appearance from their marine relatives that the former rank as a separate variety, "*gymnurus*," which derives its name from the suppression of most of the lateral scutes which distinguish the marine variety "*trachurus*."[29] The number of the plates is variable in the latter form, and Florentin[30] has found that *gymnurus*, in water of unusually high salinity, tends to go over to the *trachurus* type. This looks like very clear evidence of a

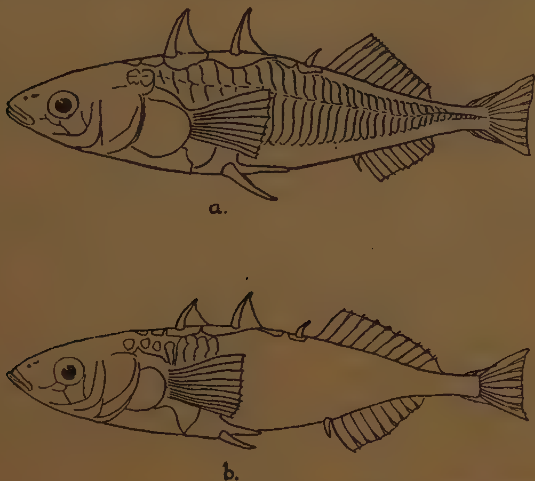

FIG. 3.—*Gastrosteus aculeatus*, the Three-spined Stickleback. *a*, the marine variety, *trachurus*; *b*, the typical freshwater form, *gymnurus* (after Tate-Regan).

structural change associated with reduction in salinity, and may be compared with the variations under changed salinity of the brine-shrimp, *Artemia salina*, which are so marked that the separate "habit forms" have even been classed as distinct species, although it has now been demonstrated that they merge into one another in accordance with alterations in salinity and other physical factors (see Fig. 92A, p. 228).

The freshwater shrimp, *Mysis relicta*, is believed to have been derived directly from the marine species, *M. oculata*, which it greatly resembles, especially in the immature stages

of the latter. The preservation of certain larval characters in the freshwater form is a feature of peculiar interest: lowered salinity is known to have a retarding effect upon development, especially in Mollusca,[26] and it may be that a key to structural peculiarities in some freshwater forms should be sought here. The whole subject of the anatomical relations between such types and their nearest marine relatives deserves exploration: certainly for the present it is impossible to make any general statement with regard to anatomical peculiarities of freshwater species.

Many of these species, however, do differ markedly from their marine relatives in virtue of two superficial features—small individual size and inconspicuous colouring; as examples, we may contrast the small, greyish shells of most freshwater Gastropods with the large and brilliant types of the marine littoral, the little grey crayfishes of sandy brooks with the great lobsters of the rock-pools, the brown brook-trout with his magnificent sea-going cousin, the salmon, the nearly transparent freshwater Oligochætes with the many-hued and variously-shaped Polychætes of the sea. These general features of small size and grey to brownish coloration, which have gone far to earn for the freshwater fauna a reputation for sparsity and monotony not wholly merited, may, in littoral types at all events, bear some relation to the relatively small dimensions of bodies of terrestrial water. It has long been agreed by competent observers that there exists some kind of relationship between the size of aquatic individuals and the volume of the medium which bounds their activities,[28] although the nature of this relationship is not clearly understood. It may depend in some cases upon facilities for concealment from enemies, which would put a premium on small size in shallow waters, or where hiding-places are limited in number and extent; in other instances, the limits of growth are no doubt determined by the available food-supply and the severity of competition for its use. In inland waters, which are more highly charged than marine with the products of organic disintegration and decay, a very large number of species have adopted the microphagous habit, which almost

always results in the production of large numbers of individuals of small dimensions. Some few freshwater carnivores, notably the pike, can grow to enormous size, while it is worthy of note that many of the peculiar endemic Invertebrate forms of Lake Baikal, a water-body of vast size and long geographical isolation (see Chapter V), rank as the giants of their respective tribes. The monotonous coloration of so many freshwater forms is probably related to the special need for inconspicuousness above-mentioned, but, in addition, pigment production is certainly strongly affected by the chemical properties of the medium, which here contains altogether a far lower proportion of inorganic salts than does the sea.

A certain definite relation seems to exist also, at least in Mollusca, between linear dimensions and salt concentration: among the marine types of the Baltic, a number show a marked reduction in average dimensions when traced from west to east (in the direction of falling salinity) across their range in this sea. The case of *Mytilus edulis* is particularly clear, for Möbius [31] found the average length of shells taken at Kiel was 8–9 cm., while those from the Stolper Bank, near Göthland, averaged only 3–4 cm.; a similar, though less well-marked discrepancy was found for species of *Mya*, *Tellina*, and *Cardium*. This diminution in size is accompanied by a loss of shell-thickness which reminds us strongly of the more extreme thin-shelled condition which characterises most freshwater molluscs: the fragile, corneous shells of familiar types like *Sphærium* and *Pisidium*, *Planorbis* and *Limnæa* form a strong contrast to the solid, limy types of *Cardium* and *Venus*, *Purpura* and *Buccinum*, and others common on the marine littoral, and even the thicker shells of some freshwater Unionidæ only attain this condition after long years of extremely slow growth. It may well be that the small dimensions of freshwater animals with calcareous shells or exoskeletons, even the absence of such tribes as Porifera Calcarea, Echinodermata, and lime-shelled Radiolaria, are related to a lime scarcity which, though *actual* in some inland waters of special type, is mainly physiological in character, as we shall see later (Chapter III, p. 64).

For many freshwater animals, and for plankton types in particular, reduction in size and in lime content are alike advantageous in view of the lower specific gravity of the medium in which they float or swim: the freshwater plankton is remarkably poor in such occasional larger forms as break the monotony of its marine prototype (see Chapter II).

Such considerations apart, the features which confer distinctive character upon the freshwater fauna are mainly physiological, and for the most part intimately related to reproduction. To understand these features, we must bear in mind the variability of the conditions to which life in fresh waters is subjected: everywhere, except in the depths of large lakes, the water temperature reflects, though on a slightly reduced scale, the variations in temperature of the air. In the sea, even littoral waters are in open communication with the central reservoir of the ocean, which maintains some thermal equilibrium, but in the inland waters as a rule diurnal, seasonal, and secular changes in temperature are far more strongly marked. Also, partly in relation to these changes, partly to influences of other sorts, the level and form of the inland water-bodies is continually subject to change. Extremes of variation occur in small ponds and mountain torrents, but in all freshwater habitats except the abyssal depths of a few lakes the fauna is dominated in its physiological relationships by the need to guard against climatic and especially seasonal changes. Among these, variations in temperature are important, yet less so than alternating drought and rainfall, which latter bring about significant changes in the physical (even chemical) condition of the water, affect its volume, and may even lead to desiccation of areas usually submerged.

Low temperatures in themselves are less inimical to life than is popularly supposed, and there are records of the tolerance of amazing degrees of cold by animals quite high in the scale of life. Freshwater fishes can survive being frozen stiff at $-15°$ C., frogs have emerged triumphant from the endurance of still lower temperatures (so low as $-60°$ C.[32]); many Rotifers and Infusoria are found in Arctic and Antarctic waters which are frozen for many months in the year,[33] and

Crustacea-Entomostraca, Hydrachnids, and even small Lamellibranchs are reported from high Alpine lakes which thaw for only two or three months annually.[34] But the endurance of very low temperatures is only possible to animals in the resting state, when all the vital metabolic activities are reduced to a minimum which resembles death rather than sleep, and even in our temperate inland waters the approach of winter is marked by the disappearance, or even the death, of many of the animals and plants alike, while those which perish leave pledges to the future, in the form of well-protected eggs or resting-bodies of some kind which can survive the winter and awake in spring to carry on the life of the race. Freshwater sponges disintegrate in autumn, setting free their gemmules which, protected by a triple coat, may sink into the mud to await the spring's return, or may be borne by currents and even blown about by winds unharmed from place to place; the pond-Hydra leaves its chitin-coated eggs to survive in like manner; the plumed colonies of Bryozoa disappear, but their firm-walled statoblasts lie buried in the mud or hooked to the stems of water-plants; water-fleas lay winter-eggs, sealed in a firm case moulted from the mother's body; beetles and water-boatmen creep into the mud to sleep; even the hardy stickleback seeks shelter under some weed-tuft or overhanging bank, while trout and minnows quit the shores for deeper waters where the season's force is slackened, and many fishes, like the tench, poise dreamily among the weeds of the bottom growth.

Even such creatures as remain active throughout the winter show the effects of its cold in the slackening of individual growth (though this may be largely due to food scarcity) and in the inhibition of reproductive processes. Almost all our temperate freshwater animals, like the terrestrial, attain their sexual phases in the spring or summer (for fuller discussion, see Chapter IV), while in very many Invertebrates, especially Rotifera and Entomostraca, asexual or parthenogenetic reproduction occurs throughout the favourable season when food is plentiful, passing later into true sexual reproduction which gives rise to resting-eggs which can survive less favourable

conditions. Such conditions are not necessarily those of winter: in the tropics, cyclic phenomena of life-histories may still be observed, and in temperate lands the signal for appearance of sexual individuals and formation of resting-eggs is frequently given by the onset of drought or a deficiency of food-supply.[35] The latent eggs, in their resistant coats, are no less capable of enduring drought and heat than cold, and protection against drought, at any rate, is even more important to the majority of freshwater animals, to littoral types in particular. The encystment of Dipnoan fishes is only the most striking case of safeguards against drought: snails near the pond margin, frogs, and other creatures adopt devices which are fundamentally similar, certain Copepoda encyst against the summer's danger in a manner which startlingly recalls the methods of the Dipnoi,[36, 37] while some midge-larvæ adopt a similar device against the cold.[38]

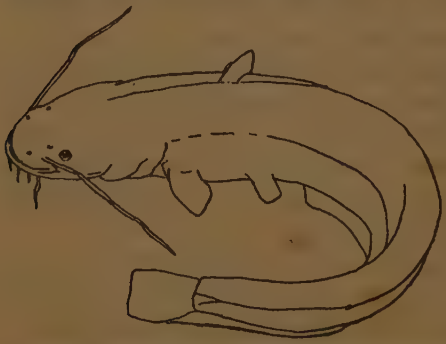

Fig. 4.—Catfish (*Silurus glanis*), an archaic type found in some European rivers (after Brauer).

The fauna of inland waters is often charged with an inherent *conservatism*, and the charge supported by references to such archaic types as the Dipnoan "lung-fishes" of African, Australian, and South American rivers, the Crossopterygii of West Africa, the North American Holostean Ganoids, and the sturgeons and Siluroid catfishes of wider distribution in the rivers of several continents; it has even been said[6] that the freshwater fauna as a whole may be regarded as an assemblage of relicts. So comprehensive an assertion could scarcely be justified, in any case, in the inevitable absence of geological evidence of the permanence of species in groups such as the delicately organised Rotifera, Cladocera, and Copepoda, which constitute a large and important

section of the freshwater fauna; on special counts, we may remark that inland waters are by no means unique in giving shelter to archaic types. In the seas, the Brachiopods *Lingula* and *Discina* have remained apparently unmodified since the Lower Cambrian epoch, the sea-lilies, and *Nautilus* and *Pleurotomaria*, are of scarcely less antiquity, while, if there is talk of fishes, it must be admitted that the most archaic of all living fishes, the Elasmobranch *Chlamydoselache*, is found in ocean waters only.

The subterranean inland waters, owing no doubt to the monotony of their conditions and to the absence of biological competition, have retained some interesting survivors of archaic stocks, modified by adaptation, of which the blind newts *Typhlomolge* and *Proteus* are the most striking examples (see Chapter IX), and some of the tropical rivers undoubtedly constitute another reserve of survival forms, while the Amphibia as a group afford an instance of survival on the large scale; but, so far as the freshwater fauna at large is concerned, there is no evidence that evolution has reached a standstill. On the contrary, our increased knowledge of local and geographical races points to a probability that the evolution of varieties and species is still very actively proceeding in the freshwater fauna as already established, while on the other hand it is continually receiving recruits from the marine littoral. Certainly this fauna is by no means static.

Further, a few special localities, lake-basins of high antiquity and comparative isolation, contain peculiar fauna, rich in species of an endemic type which seem to represent the partially modified survivors of a stock of extreme antiquity, preserved in these lakes by isolation during a period of evolution of the more modern types which now people the inland waters in general.

Bearing such facts in mind, we may substitute for the sweeping assertions too often made an acknowledgment of a certain tendency in the freshwater fauna to the preservation of archaic types and groups alongside the new. This tendency may likely be referred to the uncertainty of tenure, since frequent modification and replacement of freshwater bodies

puts a premium on the continuance of types already rigidly adapted for the survival of abrupt changes and for effective dispersal. The keynote of evolutionary changes in the fresh-water fauna has been the adaptation of physiological processes rather than of anatomical features, just as we might expect to be the case with a fauna evolving mainly from a stock already well adapted for life in a watery medium which differed from the new element chiefly in physico-chemical detail.

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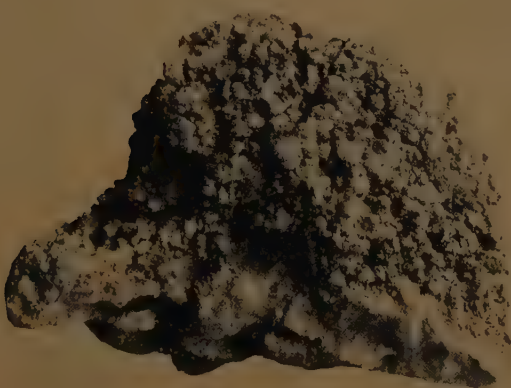
PLATE II

(*a*) Portion of a stem of *Potamogeton natans*, showing incrustation of calcium carbonate.



(*b*) Stone from the shore of a loch at Lismore, showing incrustation of calcium carbonate caused by the metabolic processes of minute lithophilous algæ.

(Both (*a*) and (*b*) are reproduced from West's "Flora of Scottish Lakes," in *Proc. Roy. Soc. Edinburgh*, XXV, ii, 1905.)

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CHAPTER II

THE COMPONENTS OF THE FRESHWATER FAUNA, THEIR ACTIVITIES IN GENERAL, AND THE INTERRELATIONS BETWEEN THEM

"You may guess what a work it were, in a discourse, but to run over those very many flies, worms, and little living creatures, with which the sun and summer adorn and beautify the river-banks, both for the recreation and contemplation of us (anglers); pleasures which, I think, myself enjoy more than any other man that is not of my profession."—IZAAK WALTON.

FOR the majority of aquatic animals, the pervasion of a liquid medium of high specific gravity has simplified one of the most urgent problems which an active being has to face, the problem of support and transportation of its own solid body; only in littoral zones of wave-wash and in the path of currents, constant or variable, this problem becomes greatly complicated by the addition of a new factor, the need to resist a dislodging force. Aquatic animals in general may be classified according to their fashion of availing themselves, in respect of support and locomotion, of the properties of the medium, or of contending with its motion. Such a classification, which, with slight modifications, may be adopted for use in freshwater studies, has been evolved in the course of hydrobiological investigations of the fauna of the seas: marine biologists divide this fauna into the *benthos*, or bottom-living animals, the *nekton*, free-swimming and migratory forms, and the *plankton*, or floating forms encountered at various depths.[1] All the classes can be recognised among the fauna of the inland waters, but we must add to them a fourth, the *neuston*, or organisms related to the surface-film of quiet waters.

Benthos.—Ground-living animals, and such as scramble

over weed, include, by virtue of the wide range of their muscular activities, the greatest variety of structural types met with in any of these faunal groups. Sluggish, plant-eating phytophiles, like pond-snails and brook-limpets--greedy, darting carnivores, like the dragon-fly and *Dytiscus* larvæ—active, scrambling scavengers, like the crayfishes and fresh-water shrimps—stone-clingers with flat bodies and radially-spread limbs, like many stone-fly larvæ--plant-scramblers with hooked antennæ, like some shore-living water-fleas and Cyclops—mud-buried current-feeders, like the pea-shells and larger mussels—more delicate microphages, that live attached and draw their food towards them by ciliary currents, like some Rotifers and Vorticellids—tube-dwellers, like the small red *Tubifex* and some midge-larvæ—net-spinners, like some caddis-worms—all these, and more, are found among the lower animals of the benthos, while many fishes feed on its rich, succulent life. Freshwater benthic types are so diverse, and vary in such intimate relation to the conditions in each water-body or reach that they are best considered separately in relation to such factors (Chapters VI, VII, and VIII).

Nekton.—In inland waters, as in the sea, "the actively locomotor organisms are mainly vertebrates"[1]: marauding brigands of these waters are some few mammalia which come to it for prey, but breed on land—chiefly otters; but for the most part, the active types are fishes, in number and variety far behind those of the sea, yet still considerable, and many of them giants in these waters whose life is mostly on so small a scale. Only these, with their stream-line bodies and strong propelling tails, can make successful headway against a current of any but the feeblest intensity, and so the nekton of the rivers is for the most part limited to fishes, though in the quiet pools and backwaters, as in the stagnant waters, beetles and water-boatmen and pond-scorpions—all carnivores—are added to their number.

Plankton.—Here, again, as in the sea, the floating population of the free medium, though small in individual dimensions, constitute an important element in the total fauna and a large item in the menu of larger types. But in the fresh

waters this element is limited in distribution, character, and quantity by certain special features of the environment, chief of which are the size of the water-bodies, the presence and force of constant currents, and the low specific gravity of fresh water as compared with saline. The most familiar features of the planktonts, marine and freshwater alike, are the transparency and delicacy of their bodies and their high proportion of surface to volume, achieved either by small size in itself (since, in two solid bodies of like shape, the proportion of surface to volume is greater in the smaller, varying in relation to the radius) or by expansion of its surface into hoods (*Phyllosoma* larvæ), " wings " (*Tomopteris*), tails (*Appendicularia*), or spines (*Zoœa* larvæ), but in all cases serving to increase the floating power. Among the plankton of the seas occur forms, such as the first three given as examples above, which are enormous in size as compared with the vast majority of Copepods, Cladocera, and even Protista which compose its mass, and these large forms drift idly in the water, sacrificing autonomy to increase of surface. A further element, of high importance in the marine plankton at certain times of the year, is constituted by the numerous pelagic eggs of fishes and ciliated larvæ of Mollusca, Echinodermata, and worms. These features go far to redeem the marine plankton from monotony, but the freshwater plankton fauna as a rule is much more uniform in type and size, and consists mostly of small and transparent-bodied Cladocera, Copepoda, and Rotifers, a number of Foraminifera and a few Dinoflagellates and Peridinians, with an almost total absence alike of free-swimming or drifting larvæ, of floating eggs,* and of large individuals with flattened and expanded bodies. These features of monotony are certainly related to the prevalence in most fresh waters of currents, usually constant in direction, which would endanger the very existence of such helpless forms by sweeping them out of their appropriate environments into new ecological conditions. In rivers, where the current is most marked, the

* Some of the plankton organisms (especially Cladocera and Rotifera) have eggs which by their structure appear to be pelagic, but they are seldom, if ever, found floating—probably because even light breezes or slight currents are sufficient to drive these very small bodies on-shore.

total plankton, even, is reduced or absent. Schröder,[2] from observations on the Oder, deduced that in general plankton-production in a river varies in inverse proportion to the speed

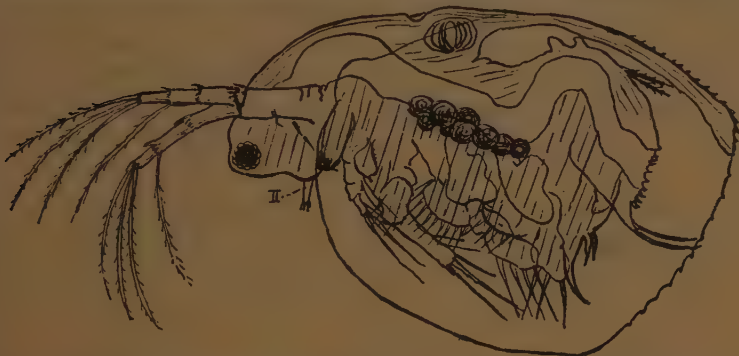

FIG. 5.—*Simocephalus vetulus*. A pond-Cladoceran which usually swims inverted, using the large second antennæ as oars. II. The small first antennæ.

of the current. The zoo-plankton, in particular, is quite unimportant in any but large and slow rivers; indeed, it may

FIG. 6.—Predaceous Plankton-Cladocera. *a*, *Leptodora Kindti*; *b*, *Polyphemus pediculus*; *c*, *Bythotrephes longimanus*.

be queried whether it be legitimate to speak of a "potamo-plankton" at all (see Chapter VII). Even in lakes, which almost all possess a definite inlet and outlet, there is usually

some constant current which would be inimical to passive, drifting creatures, while in small and self-contained ponds the conditions do not favour development of any but a limited range of types. The freshwater plankton is then, to some extent, monotonous, and composed of individuals usually smaller in size than even their next of kin in the high seas, a feature probably related to the low specific gravity of the medium. Not many years ago, the idea was general that the

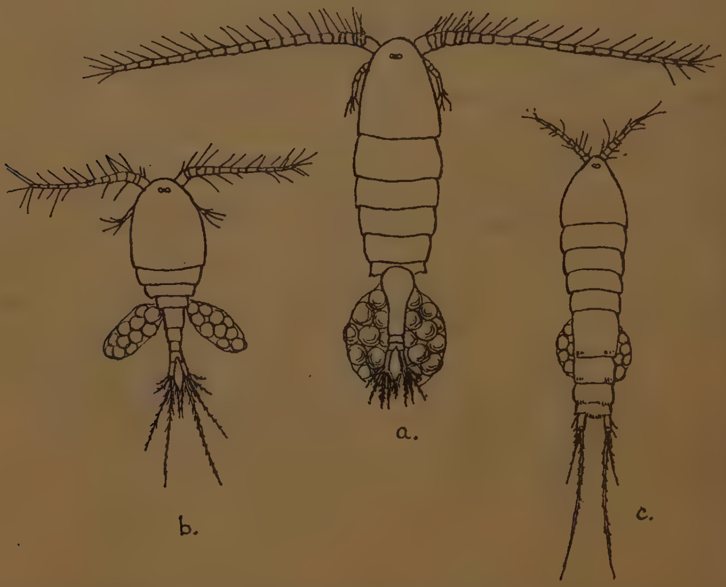

FIG. 7.—Freshwater Copepoda. *a*, *Diaptomus* (Centropagidæ); *b*, *Cyclops* (Cyclopidæ); *c*, *Canthocamptus* (Harpacticidæ). All females, with egg-sacs (after Brauer).

freshwater planktonts were for the most part passive, drifting forms, but this early view has been discredited by observations on the active movements of the animals themselves. Entomostraca show quite a variety of styles of locomotion: the Phyllopoda lie upon their backs and beat the water with their leaf-like limbs, most Cladocera (as *Daphnia*, *Bosmina*) use their long antennæ with an oar-like action, and some few types with lengthened abdomen swim rapidly, using it like a stern-

oar (as *Holopedium*, *Leptodora*). The Copepoda flap their thoracic limbs against the water, not in back-swimming, like Phyllopoda, but with a forward hopping motion: *Diaptomus* and *Heterocope* may sometimes use their long antennæ for true swimming, to change their level in the water,[3] but *Cyclops* species are merely "hoppers," and *Canthocamptus* and other Harpacticidæ are not plankton species at all, but wriggle their worm-like bodies over the stems of plants. The plankton Rotifers are active swimmers, even against a current, and the one insect-larva of the plankton (*Corethra*) swims by a lashing action of the tail, which has a "fin" of feathered bristles, and has two pairs of internal sacs into which gases are secreted, and which buoy it up in the water.[4] One small Cladoceran

FIG. 8.—Larva of *Corethra plumicornis*. a', a^2, internal air-sacs; *f*, "tail-fin" of fringed bristles.

(*Holopedium gibberum*) and one or two Rotifers have including spheres of a gelatinous secretion, which serve as floats, and also for protection against enemies (see Fig. 78, p. 198).

Neuston.—This term, applied by Naumann [3] especially to minute forms, such as bacteria and Protista, which float against the surface-film, may be extended to include all types especially associated with the film, a number of which are macroscopic. In quiet littoral waters, overhung by trees and other vegetation, the floating harvest of decaying plant-fragments, bodies of insects fallen from above, pollen-grains, and the like, encourages the presence of a number of surface-rangers which we may call the Supra-neuston. A number of Hemiptera, as pond-skaters (*Gerris*), water-measurers (*Hydrometra*), and water-crickets (*Velia*), with elongated bodies borne on long spreading limbs, dart lightly over the film in

pursuit of prey, sometimes dead, but often living, whose juices they suck out with their long beaks. The whirligig-beetle *Gyrinus*, though more thick-set, is no less active, swimming

FIG. 9.—Surface-skating Hemiptera. *a*, *Gerris najas*; *b*, *Hydrometra stagnorum*; *c*, *Velia currens*. Note the wingless condition and spread of limbs in each. *Velia currens* has a pair of dorso-lateral orange stripes, with white dots along their inner edge; *Gerris najas* has a pair of ill-defined lightish-brown stripes.

FIG. 10.—The Whirligig Beetle, *Gyrinus natator*. *a*, Dorsal view of the animal, about six times natural size; *b*, paddle-shaped third leg, highly magnified to show the flattened tarsal joints, which spread fanwise in the backward stroke.

lower, with paddle-like limbs which beat below the surface, and, that no crumbs may fall neglected from the rich man's table, the little spring-tails (*Isotomura*, *Podura*) cluster in

patches on the film, or leap suddenly from place to place by the quick straightening of their bent abdominal forks. All these, large and small, maintain their position above the film by making use of its elastic property, and their light bodies with great spread of limbs, or, in spring-tails, the diffuse contact of their hairy coats, depress it so slightly that it is not broken—except at will, for surface Hemiptera will, on

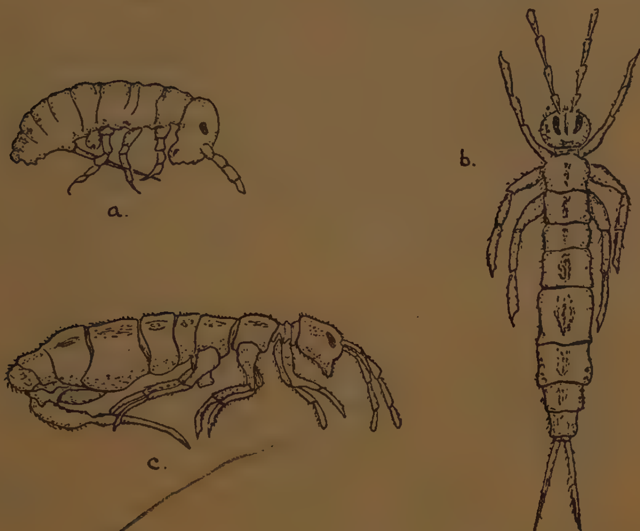

FIG. 11.—Water Spring-tails. *a, Podura aquatica*, side view (after Lampert); *b, Isotoma (Isotomura) palustris*, dorsal view, with "spring" extended; *c, Isotoma palustris*, side view, with "spring" folded (after Miall). (All magnified about 20 diameters.)

occasion, push through it and descend to lower levels, carrying their air-supply along with them.

A number of light-bodied animals may use the lower surface of the film for temporary support and attachment: *Hydra* may hang head-downward from it, and Planarian worms and pond-snails often creep against it, but these are in no sense true neuston types, but casual visitors. More intimate in their relations with the film are certain small Crustacea: *Notodromas* (an Ostracod) and *Scapholeberis*

(Cladocera) cling to it in reversed position by tufts of bristles, and oar about from place to place in search of food: the constancy of the habit in these two types is demonstrated by their reverse coloration, dark on the ventral surface, lighter dorsally, while *Scapholeberis* has a most definitely flattened ventral face with bristles admirably arranged for clinging to the surface-film.[5] Other animals often found in this infraneuston are the delicate larvæ of gnats (Culicidæ), of some midges (*Ceratopogon*), and soldier-flies (*Stratiomys*) which hang

FIG. 12.—*Scapholeberis mucronata* against the surface-film (after Scourfield).

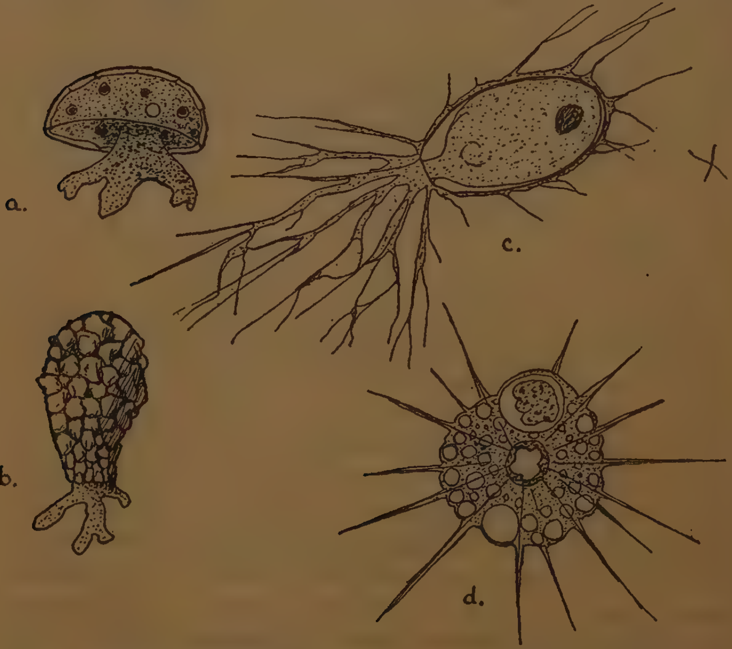

FIG. 13.—Some freshwater Protozoa. *a, Arcella,* shelled Rhizopoda-Lobosa; *b, Difflugia,* shelled Rhizopoda-Lobosa; *c, Gromia,* a Foraminiferan with chitinous shell; *d, Actinophrys,* a Heliozoan type.

suspended by a tuft of bristles around the spiracles (see later in this chapter, p. 55), as well as pupæ of these and several other Diptera (*Corethra*, *Tanypus*, *Dixa* . . .), which have trumpet-shaped respiratory tubes by which they also hang.

All these (except, of course, the pupal phases) are microphages. The infra-neuston is a company of inoffensive scavengers ; the supra-neuston, taken as a whole, is rather

FIG. 14.—Two ciliated and sedentary current-feeders, *Vorticella*, a Ciliate Protozoan ; *Floscularia*, a Loricate Rotifer.

one of pirates or of "wreckers," who probably began as scavengers, but have lost their innocence.

Among the plankton food-relations are somewhat more complex : here the main nutritional backbone is supplied by the abundant phytoplankton, largely composed of unicellular and filamentous Chlorophyceæ and Cyanophyceæ, with Diatoms and Desmids. Holozoic Protista of the plankton—such types as *Arcella*, *Gymnodinium*, *Difflugia* . . .—feed on unicellular Algæ, which they devour and digest whole, or on

Diatoms which they swallow whole, later rejecting the shells; plankton Cladocera are almost entirely vegetarian, sweeping all the smallest Algæ filtered from the current which passes between their hair-fringed limbs into their mouths to pass in an incessant stream through the short gut.[3] Exceptions to this rule are three long-bodied, active, swimming types—*Bythotrephes*, *Polyphemus*, and *Leptodora*—which are rabidly predaceous, and range through the peaceful, grazing plankton-

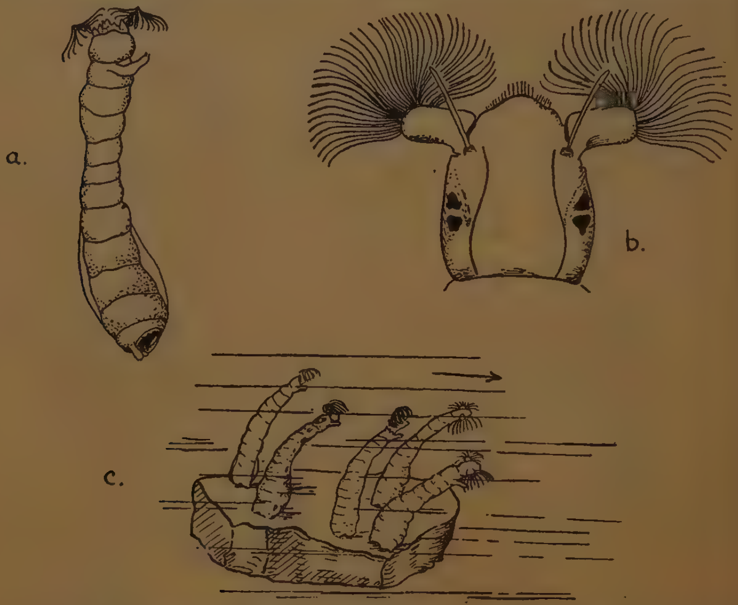

FIG. 15.—*Simulium* larvæ. *a*, A single larva of *S. reptans*, viewed from the side, to show the head-fan, prothoracic hooks (borne on a foot-like organ formed by the fusion of a pair of appendages), and abdominal sucker; *b*, dorsal view of head, much enlarged, to show the fan-like current-producing organs, antennæ, and eye-spots (after Miall); *c*, a group of larvæ on a stone, swinging out with the current of water.

herds like wolves among the flock. Copepoda are pretty well omnivorous, straining small Algæ, Diatoms, and Protozoa (even the hard-coated *Ceratium*) out of the water, while most Rotifers can feed only on the minutest of the Protista (Nannoplankton) and on such small food-particles as their ciliary currents draw to them.

Down in the benthos life is still more complex, and modes of feeding very much more varied. The line of least resistance is followed by the microphagous types which feed upon detritus floating down from upper regions; sessile current-feeders are ciliated Vorticellidæ and many Rotifers, as *Floscularia*, and Polyzoa, which form branching colonies attached to stones or weed and draw their food towards them by ciliary currents along their tentacles. Another current-feeder, the larva of *Simulium*, the sand-fly, is far more active; although it usually clings to stones in rapid brooks by its posterior

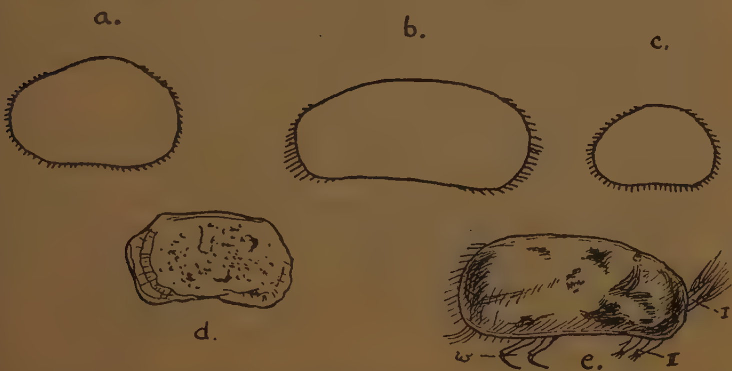

FIG. 16.—Ostracods. *a*, *Cypris virens*, outlines, after Brauer; *b*, *Herpetocypris reptans*, outlines, after Brauer; *c*, *Cypridopsis vidua*, outline, after Brauer; *d*, *Limnicythere inopinata*, a deep-water type; *e*, *Candona* (*Herpetocypris*) *reptans*, right side view, after Baird; I, II, first and second antennæ; *w*, walking-legs. All much enlarged.

sucker, sweeping in food-particles by the action of a pair of fringed head-fans, at times it moves about quite vigorously, using head and tail-suckers alternately, or catching by its claws the silken threads spun in its former progress. The bivalve Molluscs (*Sphærium*, *Pisidium*, *Unio*, *Anodonta*) are detritus-feeders, which generally lead a sluggish life half-buried in the bottom mud, from which protrudes a ciliated mantle-lip, or even a pair of siphons, along which the current is drawn within the mantle and so passed towards the mouth by the rhythmic waving of cilia upon the gill-surfaces. Slow-moving caddis-worms such as *Anabolia* and *Limnophilus* (see

Fig. 68, p. 168) are also detritus-feeders, but drag their cases over the bottom or among the plants in quest of larger particles of decaying matter, while *Hydropsyche* and several Polycentropidæ [6] are current-feeders of a very special type, since they

Fig. 17.—Snare and lair of *Hydropsyche*. *a*, Front view; *b*, side view, from a specimen which had made its lair against the side of a glass tank (after Shelford).

spin nets to catch the particles of dead or living food-matter borne upon the stream (see Chapter VII).

Tubifex and other little Oligochætes are detritus-feeders which play an important part in the economy of the fresh waters, since they bury themselves head downward in their burrows, with tails protruding, and eat the putrifying organic matter of the mud below the surface, transporting the waste above in their excreta, and thus performing a function very much like that of the earthworms to which they are related.

Fig. 18.—*Tubifex* in the bottom mud (after Needham and Lloyd).

Few animals feed directly on the leaves or stems of growing water-plants: the water-bears (*Macrobiotus*, *Echiniscus* . . .) actually pierce the tissues of Bryophytes by means of their little chitinous teeth, and suck the juices through the muscular pharynx, and some freshwater snails, especially *Ancylus*, rasp off the Algæ clinging to the stones, but most aquatic plant-feeders seem to live on already detached particles which are beginning to decay, and even the pond-snails probably derive

most of their sustenance from microscopic organisms which coat the surface of the plants on which they crawl.

Predaceous animals of the benthos vary greatly in the methods which they adopt: most interesting are perhaps the ambush types, such as the lurking nymphs of some large dragon-flies (Libellulidæ), that sprawl half-buried in the mud, ready to seize some juicy worm or larva by shooting out their

FIG. 19.—Some common freshwater Gastropods (all slightly enlarged to scale, about $1\frac{1}{2}$ times). *a*, *Ancylus fluviatilis*; *b*, *Limnæa stagnalis*; *c*, *L. pereger*; *d*, *L. auricularia*; *e*, *L. truncatula*; *f*, *Planorbis corneus*; *g*, *Pl. albus*; *h*, *Physa fontinalis*.

long prehensile "masks." The nymphs of larger stone-flies (*Isogenus*, *Dictyopteryx* . . .) are flat-bodied types with spreading legs for clinging under stones; near them are often found the mayfly larvæ (*Ecdyurus*, *Baëtis* . . .), and on these and other more defenceless larvæ and worms they feed voraciously, crushing the bodies between their strong, toothed mandibles. Some of these larger mayfly larvæ, too, especially the stone-

clinging types, are actively predaceous, and may even feed on weaker members of their tribe, that creep or burrow in the mud (*Ephemera*, *Ephemerella*). These last-named, and the swimming types (*Chlœon* . . .), are all carnivorous, and feed on the small creatures they find in mud or on the leaves of water-plants. The smaller Ephemerids are microphagous. (For figures of stone-fly and mayfly larvæ, see Chapter IV. Even some Diptera are carnivores: *Tanypus* has a worm-

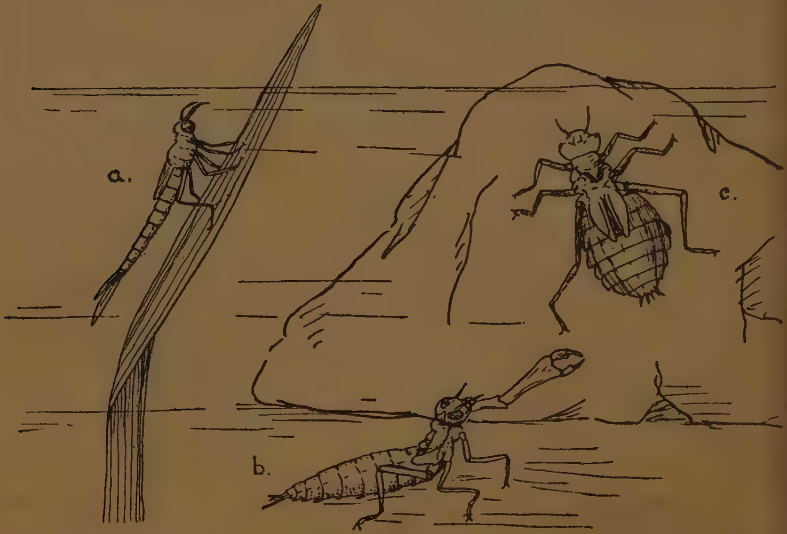

FIG. 20.—Dragonfly nymphs. *a*, Nymph of *Calopteryx*, with three caudal gills; *b*, nymph of *Æschna*, with mask outspread for seizing prey; *c*, sprawling nymph of *Libellula* (all about natural size).

like larval form which builds a little tube of mud for shelter, but often leaves it to swim with looping movements or crawl among plants, pushing itself on by a crutch-like "foot" (really a pair of joined thoracic legs), and preys on other insects and Crustacea. The delicate, transparent body is sometimes seen to be coloured red from undigested portions of the bodies of *Chironomus*, a peaceful detritus-feeder.

Leeches are carnivores of a peculiarly unpleasant type, for they live by sucking the blood of Molluscs, worms or insect-

larvæ, or even of Vertebrates: when not feeding, they prefer to rest attached by their suckers to the under-sides of stones half-buried in the mud. *Hirudo*, *Aulostomum*, and *Herpobdella* swim, if disturbed, with undulating movements of the body, but the Clepsinid types (*Glossiphonia*, *Helobdella* . . .),

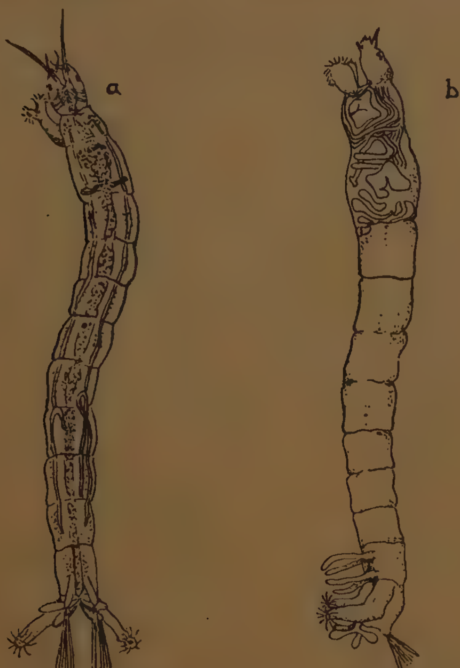

FIG. 21.—*a*, Larva of *Tanypus*, showing the "crutch" formed by the fusion of the prothoracic legs, four "abdominal gills," and a pair of hook-fringed appendages on the last segment; *b*, larva of *Chironomus plumosus*, with two pairs of hooked appendages on prothoracic and last abdominal segments, two pairs of "blood-gills" on the penultimate segment, and "anal gill-tuft" on the last.

with broader bodies, usually crawl upon their suckers, arching like looper-caterpillars (see Fig. 38, p. 80). The little "whirl-worms" (*Planaria*, *Polycelis*, *Dendrocœlum* . . .) that shelter in the daytime under stones, their flattened bodies closely pressed against them, prowl by night and in the half-darkness in search of worms or soft larvæ, which they suck dry by the inversion

of the pouch-like pharynx; they are greedy for the blood of any Vertebrate, and even in the daytime will crowd to the spot where it oozes into the water. Hydrachnidæ suck the juices of soft-bodied insects and Crustacea, fixing themselves upon the less protected intersegmental areas, where they often form a fringe of little scarlet beads. Most considerable of all the carnivorous Invertebrates are perhaps the beetles: the larger Dytiscidæ and their larvæ, with their strong piercing and sucking mandibles, from which a groove conducts the juices of the prey directly into the mouth, do terrible destruction among the benthos, as every unwary amateur of the aquarium has cause to know. Many Hydrophilid beetles are partly vegetarian, but they seem to prefer animal food, and their carnivorous larvæ are no less greedy than the Dytiscidæ. It must be added—to redeem the character of the Coleoptera in general—that many aquatic forms (*Hydrobius*, *Helophorus*, most small Hydrophilidæ, etc.) are strictly vegetarian.

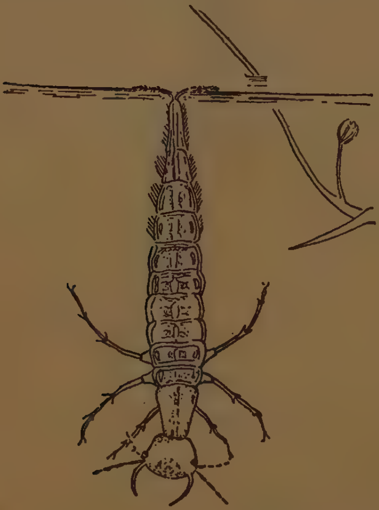

FIG. 22.—Larva of *Dytiscus marginalis*, breathing at the surface, as it hangs inverted by its abdominal appendages. Note the strong, curved mandibles which project forwards.

Some of the most highly specialised of all freshwater carnivores are found among Hemiptera: the water-boatmen, with their hair-fringed legs (*Corixa*, which swims like a Dytiscid beetle, and *Notonecta*, the "back-swimmer"), feed, like their cousins of the neuston, partly on dead bodies, but pond-scorpions (*Nepa*, *Ranatra*) hunt for living prey, insects and water-fleas, and seize them by the strong forelegs with powerful folding blades which have earned for the possessors their special title. These are wasteful and untidy feeders, sucking

juices through their beaks, and rejecting a great part of the prey, but what need to fidget over the disposal of scraps when those pickers-up of unconsidered trifles, the water-scavengers, are never far to seek? Malacostraca hold this office by hereditary right; in the fresh waters the little

FIG. 23.—Three predaceous aquatic insects. *a*, *Dytiscus marginalis*, ♀; *b*, *Notonecta glauca*; *c*, *Macrocorixa geoffroyi* (ventral view). Note the wide spread of the hair-fringed swimming legs in each. (*b* and *c* are drawn about twice natural size, *a* is rather less enlarged.)

Amphipods and Isopods (*Gammarus*, *Asellus* . . .) are far more general in occurrence than the larger crayfishes, which are confined to certain clear and sandy brooks, mainly in limestone areas.

Hemiptera and carnivorous beetles (though not the beetle-

larvæ, which as a rule are crawlers), and, to some extent, crayfishes too, really belong not to the benthos but to the nekton of the calmer waters. In waters of both types, rapid and calm, the strongest and largest of nekton creatures are the fishes, which mostly, when adult, prey on the benthic life without too much discrimination, and even on smaller fishes. The pike, in quiet ponds, grows to enormous size on such a diet; trout devour minnows, and even, not infrequently, turn cannibal. Most fishes in their younger stages feed on the transparent creatures of the plankton, and derive much nourishment especially from the copious drops of oil within their tissues, which they themselves obtain from the phytoplankton, and which serve to buoy up the bodies of these planktonts, while giving to some of the Entomostraca those brilliant red and orange colours we so often see in limnetic types.[7]

FIG. 24.—The pond-scorpion (*Nepa cinerea*) hanging from the surface-film by its respiratory tube. Note the strong, curiously-modified fore-legs. (Enlarged about 1½ times.)

So, at the base of all aquatic life, providers of its carbonaceous matter by photosynthesis, we find the plants: even detritus-feeders owe much of their substance to vegetable decay, and carnivores prey upon direct plant-feeders as well as on these less fastidious types. Carnivores as a rule do not hunt carnivores—not on any principle of honour among thieves, but that their skins are often leathery or chitinised, their muscles too hard for easy digestion; but there are exceptions. Even the trout, known for a dainty feeder, will eat leeches and beetles or Hemiptera, in barren pools where life is scanty: the writer has had specimens with all these in their stomachs from plateau-ponds in the Welsh hills. Fishes

are preyed upon by water-birds, and otters, and each other, and most of all by man: the products of man's bodily activities pass, through the soil and drainage-channels, largely into the inland waters, and putrifying bacteria break them down, and nitrifying organisms then build up the waste into nitrites and nitrates, soluble compounds which the plants combine with products of their photosynthesis into the stuff of life again. . . . "The wheel has come full-circle."

The pivots of this wheel of life are assimilation and respiration, anabolism and catabolism—a synthesis of the stuff of life

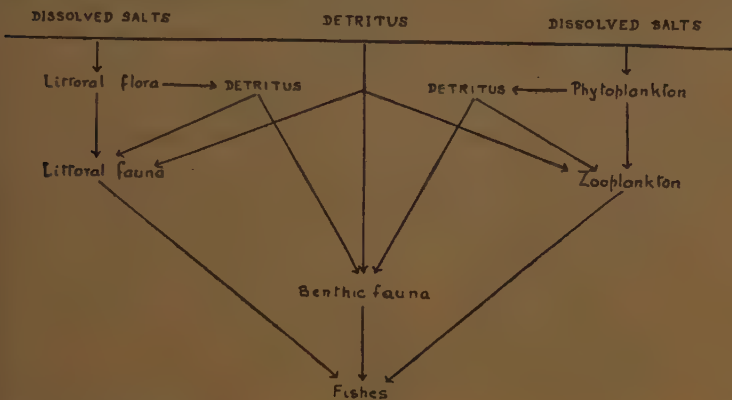

FIG. 25.—Scheme of food-relations in freshwater (partly after Naumann).

and a slow burning which releases energy, and as companion to our study of nutritional devices we must trace the expedients by which freshwater animals obtain their oxygen.

For littoral animals of simple structure, without hard coatings, and of no great size, the problem is a fairly easy one. The ambient medium, in contact at its surface with the air, ventilated by currents, and further aerated by the oxygen-freeing chemistry of green plants, contains the necessary oxygen in readily accessible form, and gas-diffusion easily takes place through a moist and permeable covering membrane. Respiration of this general and unlocalised type takes place in Protozoa, *Hydra*, Rotifers, and many worms, and even in some few insect-larvæ, such as *Tanypus*, in which the spiracles

are rudimentary and have no stigmata. But with increase of bodily complexity, chitinisation of the surface, or adoption of the sheltering habit, comes a need for special thin-skinned breathing organs. In some freshwater types the respiratory function is handed over to organs already adapted for the fulfilment of another duty, whose branched or leaf-like contour gives them an increase of surface which facilitates exchange of gases. Such are the tentacles of the lophophores of Polyzoa, which project beyond the sheltering tubes to gather in the food-current (see Fig. 42, p. 84), and in like manner the leaf-like thoracic limbs of Entomostraca serve for respiration as well as for locomotion and the production of a feeding-current.

Some Dipteran larvæ have little finger-like projections (see Fig. 21, p. 45) from the posterior segments, which many biologists have assumed to function as respiratory organs: in the case of *Chironomus* larvæ of the *plumosus* group, at least, it has been definitely proved that no especially intense exchange of gases takes place at the surface of these so-called "anal gills,"[8] and in some other species they are certainly of very little use in breathing, even if they are used at all, since varnishing their surface does not appear to incommode the animal[9]: probably the term "gills" is a misnomer.

FIG. 26.—*Valvata piscinalis* (after Simroth). *op*, operculum; *ct*, gill.

In larger animals, including some Mollusca, higher Crustacea, and fishes, the special organs of respiration are "gills," very various in structure, but alike in being thin-skinned outgrowths from the body-wall, copiously supplied with blood-vessels. The Streptoneurous Gastropods (as *Valvata*) have simple plumose gills, but the majority of water-snails belong to the Pulmonata, and possess an enlargement of the collar-cavity, richly supplied with blood-vessels and

functioning as a "lung." These snails must therefore climb out of the water or creep against its surface to renew the air within this chamber, although *Limnæa* in the abyssal depths, as we have seen, manages very well when the air-chamber is filled with water. Some marsh-frequenting tropical snails (Ampullariadæ) have two chambers in the mantle-cavity, one containing a gill, for aquatic respiration, while the other half serves as a "lung," and has a long siphon-tube which can be thrust up into the free air. Lamellibranchs have large and very complicated gills, past which a current of water is maintained, as we have seen, by ciliary action; *Pisidium* has a

FIG. 27.—*Ampullaria:* a tropical marsh-dwelling snail. *a*, Dorsal view; *b*, Diagram T.S. passing through the mantle cavity; *s*, siphon tube; *l*, "lung" cavity; *g*, gills (after Semper).

single siphon, which it thrusts out of the mud to the clear water; *Sphærium* has two, and the freshwater mussels have only slightly spout-like fringed projections of the mantle-folds.

Smaller Crustacea respire, as we have seen, by the leaf-like thoracic appendages, and probably in some cases over much of the general body surface, but in higher types there are rows of plumose gills projecting from the limb-bases, and protected by the arching lateral flaps of the strong carapace in a gill-chamber through which the baling action of the maxillary scaphognathite draws a constant current.

The gills of fishes are set between the pharyngeal gill-slits, and the movements of jaws and protective operculum combine

to keep continual exchange of water proceeding through the arches. The mechanism by which this is achieved is a pumping action of mouth and opercular flaps alike: not the straightforward swallowing of water, to trickle out backwards through the gill-slits, but a double action which can be performed independently by either jaws or operculum if the other be thrown out of action.[10] This pumping action has especial power in the Cyclostomes, which, as their alternative title of "Marsipobranchs" denotes, have pouch-like gill-chambers, capable of very vigorous suction—a useful modification for creatures whose sucking mouths are generally fully employed in attaching them to the larger fishes upon which they are semi-parasitic.

Fishes which live in muddy or swampy reaches, where the turbidity of the water or reduction of its oxygen by organic decay render aquatic respiration difficult, often have special adaptations, accessory to the function of the gills, enabling them to take air at the surface. Such cases are most frequent in the tropics, but even in our native pools the carp may often be seen rising to the surface, apparently to gulp in atmospheric air, though perhaps the object is to reach the better oxygenated surface-water. Lung-fishes and Holostei use the air-bladder for gaseous respiration, and its inner surface is highly vascular and thrown into complicated folds, almost like a true lung; *Ceratodus*, rising to the surface in Australian swamps, is said to emit a sound like the roaring of a bull, as it exhales the used-up air. In several American and Indian fishes (*Saccobranchus*, *Singio*, *Amphipnous*) there are air-sacs leading from the branchial cavity, analogous but not homologous with the swim-bladder of Dipnoan types; these, too, breathe at the surface, and *Amphipnous* can wriggle in wet grass like an eel, which it rather resembles in form until the air-sacs are inflated, on which occasion it looks more like a balloon—and explodes like one, if accidentally trodden on. A few fishes of Asiatic and African swamps and rivers have accessory respiratory organs of a different type, vascular, spongy outgrowths just above the gills, in a protecting hollow (*Clarias*, *Heterobranchus*); in *Anabas*, the Indian climbing perch, which

spends long periods in dry air, these outgrowths are supported by strong bony plates. Perhaps the most remarkable of surface-breathing methods is adopted by one European and several Brazilian fishes (*Cobitis*, *Callichthys*, etc.), which literally swallow air at the surface, absorb its oxygen in the intestine, whose mucous membrane is raised into vascular folds, and expel waste gases in bubbles through the anus.[10]

An even greater interest may be found in the study of those aquatic insect types which, in abandoning the terrestrial life, have found it necessary either to patch and remodel the old breathing apparatus or to supersede it by new. The simplest device, and one successfully adopted by many adult aquatic insects, is the protection of the spiracles by arching wing-cases or chitin folds, and the inclusion of an air-bubble by surface tension between these folds or in a hairy felting. This device is seen in great perfection in the great diving-beetle (*Dytiscus*), which has its reservoir beneath the elytra, abutting on the two enlarged posterior spiracles. *Hydrophilus*, another water-beetle, has an additional reservoir situated in a funnel-shaped depression between head and thorax, extending into grooves behind the thighs. Other adult aquatic insects ring the changes on small variations in position and control of the air-reservoir and safeguards against the flooding of the spiracles with water: the series of adaptations found in the Hemiptera is perhaps most interesting of all. *Gerris* and others which skate upon the surface rely upon the presence of a short, velvety pile to keep their bodies dry: *Velia currens* may sometimes break through the film and hang below it, never wetted, in virtue of this pile. *Notonecta* carries the tendency still further, swimming inverted or hanging from the film, still in its coat of air, or even springing up through the film and falling back into the water. *Corixa* goes below more frequently, and seldom comes above the film, but at long intervals pushes just so far through it as to breathe the air by its thoracic spiracles. *Nepa* and *Ranatra* stay below entirely, but have a long respiratory tube formed by the apposition of two hollowed spines growing from the tip of the abdomen, which tube is pushed through to the surface, and conducts

air to the solitary pair of posterior spiracles (see Fig. 24). These Hemipteran types form an adaptive series of high interest, since they show a parallel specialisation in their feeding habits, from scavenging at the surface to hunting prey among the submerged weeds.

Larvæ of insects, more adaptable than the adults, have more variety of respiratory mechanisms, and some of them have even become quite independent of atmospheric air. The larvæ of most beetles are not so, but take in air through the posterior spiracles, hanging at the surface by their tails; *Gyrinus*, with its fringe of gill-like organs (see Fig. 46, p. 95), is an exception to the general rule. Dipteran larvæ, with a few exceptions, mentioned above, also breathe atmospheric

FIG. 28.—*a*, *Culex* larva hanging by its abdominal respiratory tubes; *b*, *Culex* pupa hanging by the thoracic trumpets (both enlarged about 6 times).

air, and small, light-bodied forms generally have the spiracles raised on some sort of cone or papilla which is fringed with hairs to grip the surface-film, as in the larvæ of Culicidæ, *Stratiomys*, and a number of others. While all such larvæ and the pupæ of some of them hang reversed from the surface-film by the tip of the abdomen, the pupæ of Culicidæ hang by a pair of tubes projecting from the thorax, known as "respiratory trumpets," which allow the air to pass through to the spiracles. The rat-tailed maggot (*Eristalis*), which lives in foul and turbid waters, has a long breathing-tube, rather like that of *Nepa* superficially, but in this case the outer tube encloses a delicate siphon, which prolongs the tracheæ far beyond the body; *Ptychoptera*, another swamp-dweller, has a very similar device.

Most of the aquatic larvæ of insect-groups less highly organised than Diptera have become fully adapted for breathing under water, and, except for those with very small and delicate bodies, where respiration is unlocalised, bear organs, plate-like, thread-shaped, or tufted, commonly called "gills," which are kept waving by the water-current or by movements of the body. These are not "blood-gills"; they merely serve to enclose under a delicate integument a fine network of ramifications of the tracheæ, which have no open stigmata, but exchange their gases with those in solution in the water

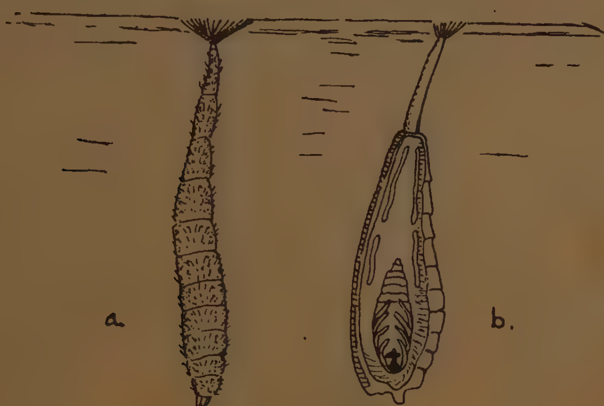

FIG. 29.—*a*, Larva of *Stratiomys*, hanging at the surface; *b*, pupa of *Stratiomys* within the larval skin (partly after Swammerdam).

by diffusion. Such tracheal gills are found in caddis-worms, in larvæ of Agrionid dragon-flies, Sialidæ, Ephemerids, and stone-flies, and vary greatly in position and arrangement. Agrionids have three pointed, plate-like gills projecting from the tip of the abdomen; Sialidæ have paired, jointed rods from each abdominal segment except the eighth and ninth, while those of the tenth segment are fused together into a fringed "tail"; Ephemerids bear hairy filaments in tufts, or plate-like organs singly or in pairs upon the abdomen, and large stone-fly larvæ have tufts of filaments on the thorax and at the base of the long caudal style, while smaller larvæ have no tracheal gills at all. Large Trichoptera have tufts or single

filaments on the abdominal segments. (For figures, see Chapter IV). The diversity of form and situation of these respiratory organs in aquatic insect-larvæ is strongly suggestive of an origin by separate experiments in adaptation to the new habitat on the part of creatures formed for life in air.

Most curious of all respiratory arrangements are those of Libellulid dragon-flies and of *Donacia*, the leaf-eating beetle, which represent extremes of adaptation along two widely divergent lines. Libellulid larvæ have the rectal chamber

FIG. 30.—The Rat-tailed Maggot (larva of *Eristalis*), creeping on the mud with its telescopic breathing-tube raised to the surface.

very much enlarged, and lined with a rugose membrane in which runs a close network of tracheæ; the action of strong muscles pumps the water into this chamber, where diffusion of gases takes place, and the violent expulsion of the water jerks the whole body forwards, rather like the squirting mechanism of a cuttle-fish. *Donacia* has a pair of slender spines projecting backwards from the abdomen, in which run extensions of the tracheæ, opening to stigmata close by the points; the larva bites holes in the roots of water-plants, or pierces them with its spines, which are then thrust well into

the tissues of the plant, to tap the oxygen in its air-spaces. In this case, the plant is undoubtedly the loser, as is generally the way in transactions between plants and animals in the fresh waters; examples of association for mutual benefit are very rare, but one clear case is that of the alliance between *Hydra* and those Algæ, brown or green (*Zooxanthella*, *Zoochlorella*), which live within its cells and supply the products of their assimilation in return for shelter.

Examples of organic partnership or commensalism seem to be far scarcer in fresh water than in the sea, but parasitism is a common thing, ranging from mere temporary fixation and blood-sucking, like that of lampreys, to the internal parasitism of Trematodes and Cestodes. The subject is too vast for discussion here, but mention must be made of the frequency of epiphytism on the part of sessile organisms, such as Polyzoa and Vorticellidæ, in still waters. In many ponds it is a common thing to find the bodies of little Crustacea, pond-snails, and even fishes, overgrown with masses of these epiphytes, especially *Epistylis*, which, at first profiting by the active motion of their host, often end by impeding motion and respiration too, and so come to kill the goose that laid the golden eggs.

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CHAPTER III

THE LIFE OF INLAND WATERS IN ITS RELATION TO THE CHEMICAL AND PHYSICAL PROPERTIES OF THE AMBIENT MEDIUM

"Concerning which you are to take notice, that it is reported by good authors, that grasshoppers and some fish have no mouths, but are nourished and take breath by the porousness of their gills, man knows not how."—IZAAK WALTON.

IT has somewhere been said that probably no really new idea has been conceived by any man since the discovery of the use of fire, and certainly the words quoted above, written in 1654, foreshadow, though somewhat crudely, a "modern" theory which has been the subject of heated controversy during the last twenty years. "Pütter's Theory," that many aquatic animals derive at least a great part of their sustenance from organic matters in solution in the surrounding water, was based upon the calculated insufficiency of solid food, suspended in sea-water, for the needs of microphagous animals, which, on the basis of these calculations, would need to filter enormous quantities of water to extract a modicum of food. But recent improvements in methods of plankton collection have established the vast importance of the "nannoplankton," consisting of minute unicellular Algæ and bacteria, so small that they pass through the meshes of the ordinary plankton-nets, yet in aggregate often exceeding the net-plankton by many times its bulk, so that the supply of living food for current-feeders is certainly very much greater than was previously supposed. Direct observations on the minute Crustacea of the plankton, which, of all the freshwater fauna, might be considered most likely to absorb their nourishment in liquid form from the element which surrounds them, have convinced

the observers that these animals do incessantly strain out the Algæ from the water as it passes between the bases of their limbs, and in Copepoda and Cladocera solid material is usually to be found in the gut, among which the valves of Diatoms and fragments of green Algæ are very often recognised.[1, 2] Further, the increase and decrease in numbers of the zooplankton in lakes bear a definite relation to the sequence in the phytoplankton, whose significance cannot be overlooked; this has been beautifully demonstrated in the case of pond Rotifers by Dieffenbach and Sachse, whose figure we reproduce. Even a definite demonstration of solid feeding

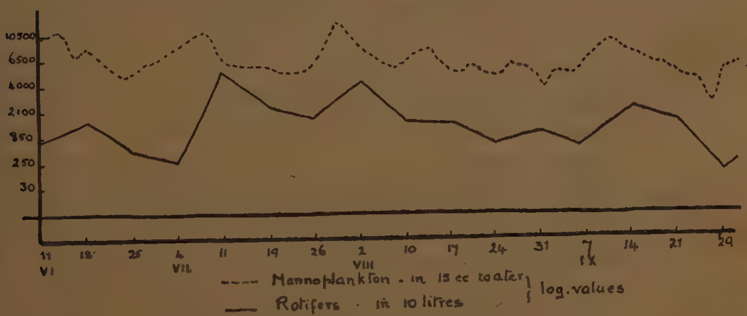

FIG. 31.—Relation of the numbers of Rotifera in a Saxon pond to the development of the nannoplankton (after Dieffenbach and Sachse).

does not of course exclude the possibility that liquid nourishment may also be absorbed, but conclusive proof of this is a difficult matter, involving the use of elaborate chemical methods, and though some marine biologists incline to a belief in the validity of Pütter's Theory (for a discussion of the evidence, see [3]) it cannot be considered to be established so far as the fresh waters are concerned. Certain experiments with freshwater animals, indeed, have given definitely negative results. Dakin and Dakin, working with goldfish,[4] have been unable to confirm assertions made by Pütter relative to their absorption of liquid foods, and attempts at rearing Cladocera on nourishment in this form have proved a failure,[5] while Křiženecký's demonstration of the growth of tadpoles in liquid culture-media has been criticised on grounds of the

probability that bacterial development may have provided an intermediate nutritional supply.[5] But the whole matter is one of such complexity that it is impossible to claim that all the necessary evidence is as yet to hand.

Whatever be the final conclusion, the importance of plant life to the aquatic fauna as a fundamental source of their organic food-supply is in no wise diminished, and the solution-content of the water is vital to the existence of fauna and flora alike.

Submerged aquatic plants depend directly for their maintenance upon inorganic substances dissolved in the surrounding water, and the raw materials which they take from it are as follows:

A. Oxygen, for use in respiration.

B. Essential food-stuffs:

1. Nitrates and nitrites of various bases, sodium, potassium, etc.;
2. Carbonic acid, either in free solution, or "half-bound," as bicarbonate;
3. Phosphates;
4. Silica, which may be present as colloidal silicic acid, or may be decomposed by plant activities from the silicates of suspended particles of clay;
5. Calcium carbonate.

While all these substances are normally present in the fresh waters within the zones of plant life, their quantity is subject to variations which are of great importance, and which often bear both a causal and a consequent relation to the fluctuations in abundance of aquatic life.

In the matter of the dissolved gases, oxygen and carbon dioxide, the surface waters naturally tend to an equilibrium with the atmosphere in which the balance is held by the prevailing conditions of temperature, since the volume of gas which can be dissolved by a given quantity of water varies in inverse relation to temperature, pressure being constant. A reasonably pure lake or river-water at the surface approximates to saturation values for dissolved atmospheric gases: thus, pure water at normal pressure absorbs from the air, at 0° C.,

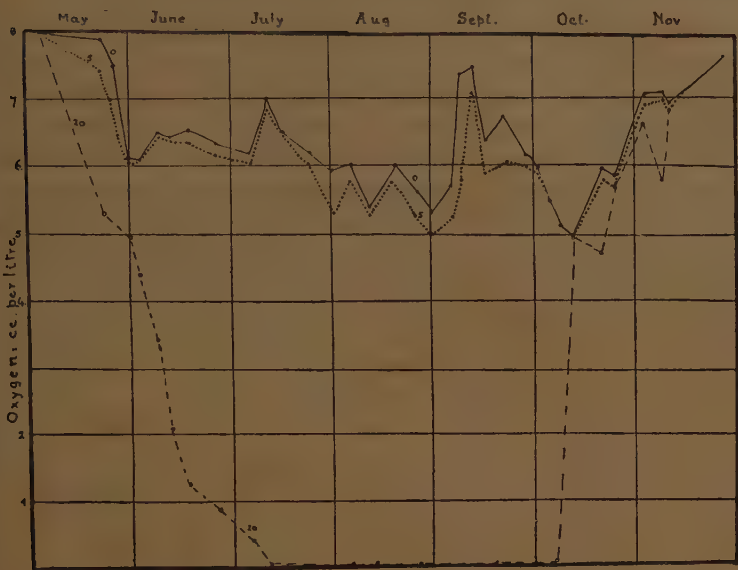

FIG. 32.—Dissolved oxygen in Lake Mendota, 1906 (after Birge and Juday). The figures attached to the curves indicate the depth in metres. The oxygen is expressed in c.c. per litre; thus there is an apparent fall in oxygen-values in the 0–5 metres zone in summer, although actually oxygen-saturation at the given temperatures was maintained during most of the period May–September, and supersaturation occurred in the second weeks of July and September (see Fig. 32A).

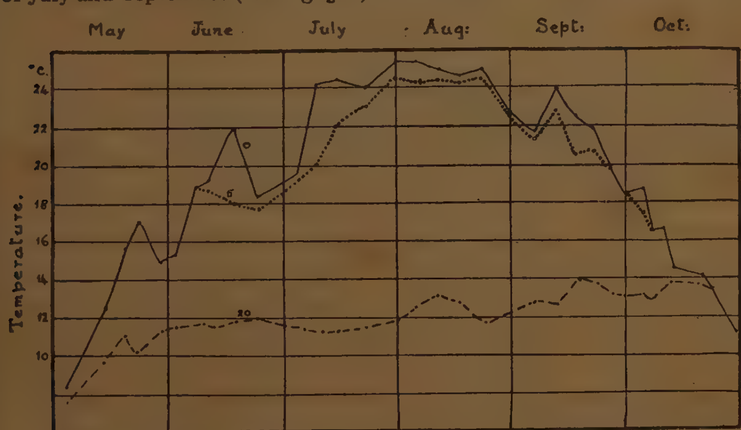

FIG. 32A.—Temperature of the water in Lake Mendota, 1906 (after Birge and Juday). The figures attached to the curves indicate depths in metres.

9·7 c.c. of oxygen, 7·77 c.c. at 10° C., and only 6·28 c.c. at 20° C.

A little below the surface, however, and to some extent throughout, these relationships are considerably altered by the process of organic activities. Plants, like all living beings, reduce the atmospheric oxygen in respiration, freeing at the same time carbon dioxide, but this effect is heavily outweighed at most times by the converse activity of carbon assimilation,

FIG. 33.—Free carbon-dioxide in Lake Mendota, 1906 (after Birge and Juday). The figures attached to the curves indicate depths in metres. Spaces above the zero-line show negative carbon-dioxide, or the alkalinity, and spaces below, the acidity in terms of carbon-dioxide (c.c. per litre).

and where green plants live the tendency is towards a rise in oxgyen values, together with a corresponding fall in carbon dioxide. Still waters, where plant growth is rich, are frequently in a state of supersaturation with regard to oxygen, and the slow rise of oxygen bubbles to the surface is a familiar sight on sunny days. The reduction of carbon dioxide, though more difficult of demonstration, is no less real, and both processes prevail in daytime, when light-energy is available, as against the night; also in summer, when there is more

light, and more green growth is present, as against the winter, when both factors are reduced. Records of variation in oxygen-content of freshwater lakes [6, 7] show that here, as in the sea, there is a well-marked seasonal cycle, highest values prevailing in the warmer months of plant-activity, while rises in the carbon-dioxide curves correspond with the zooplankton maxima.[8] (N.B.—No reference will be made throughout this chapter to the special conditions which obtain in lakes below the zone of green plant-life, or in polluted waters; both will

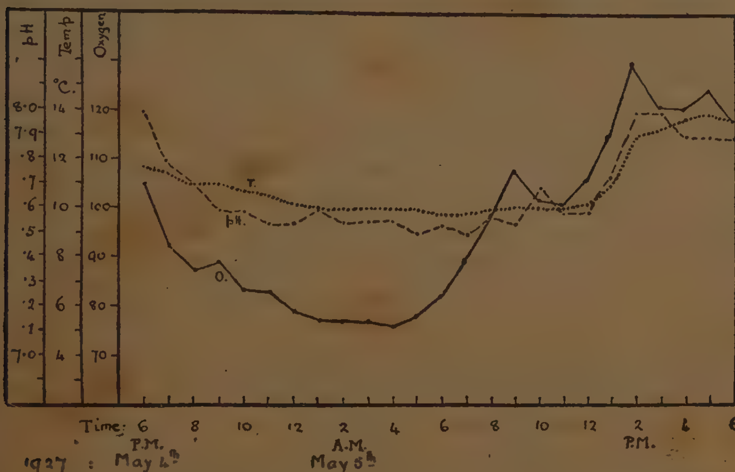

FIG. 34.—Diurnal changes in oxygen (O), *p*H, and temperature (T) in the River Itchen, May 4–5, 1927. (Oxygen as percentage of saturation.) The irregularity in the curves at about 9 p.m. was coincident with a heavy thunderstorm. (After Butcher, Pentelow, and Woodley.)

receive discussion later—Chapters VIII and X). In rivers no such annual curves have been established, but an interesting recent discovery is the diurnal curve of dissolved oxygen in streams, which, as might be expected, takes in lesser degree the form of the seasonal curve, day and night corresponding in little to summer and winter [9]; doubtless diurnal variations will be found even more clearly marked in stagnant waters.

The quantities of inorganic salts, in the form of nitrates, nitrites, silicates, and phosphates, contained in the normal fresh waters are very low; indeed, all but the first-named can

only be estimated in parts per million, and for this cause, which renders the determination of their variations a tedious matter, these have been but little studied, though the few observations which are on record show them to be by no means devoid of interest. Nitrates bulk larger, and may usually be reckoned in parts per 100,000; these salts are used by plants in proteid formation, and so when rapid growth begins in spring much of the nitrate-content of the water is removed from solution. It is restored during autumn and winter, when so many plants die down, and bacterial action breaks down their proteids, through ammonia and kindred substances, to build them up to nitrites and once again to nitrates. The nitrate-content of the fresh waters therefore tends to fall after the vernal outburst of life sets in, to reach minimum level in high summer,[7, 10] and the annual curves are pretty nearly the reverse of those of oxygen, while the ammonia-content also tends to be lowest when oxygen is at its maximum.[9, 11] Phosphates in free solution, like the nitrates, decrease during the spring, and the phosphate-content may remain at practically *nil* all summer; the winter maximum follows the decline of plant activity, and these salts are largely released in the form of animal-excreta, from which they can be readily dissolved.[12, 13]

The case of silica is interesting: the seasonal variation is roughly in agreement with that of nitrates and phosphates, but shows a definite relation to the periods of maximum development of the Diatoms, whose flinty valves are impregnated with the substance; the special features of the silica-curve are a marked fall corresponding with the autumn maximum of Diatoms, and a very noticeable increase just after the late spring development of plankton Crustacea, which feed upon the Diatoms, but reject their valves.[14]

Calcium carbonate in solution diminishes very markedly during the season of greatest plant activity; the plants abstract carbon dioxide from the water and the soluble bicarbonate, with the result that the insoluble acid carbonate is precipitated. This often forms scaly coatings on the leaves and assimilating stems of water-plants (see Plate II), and some of it is deposited

as a fine powdering upon the bottom, though for the most part calcareous bottom-deposits are derived from the shells and skeletons of dead animals. Re-solution of the carbonate seems to take place in the deeper layers of the water, and convection currents finally restore the quantity in the upper portion, after the season of greatest plant-activity is over.[7]

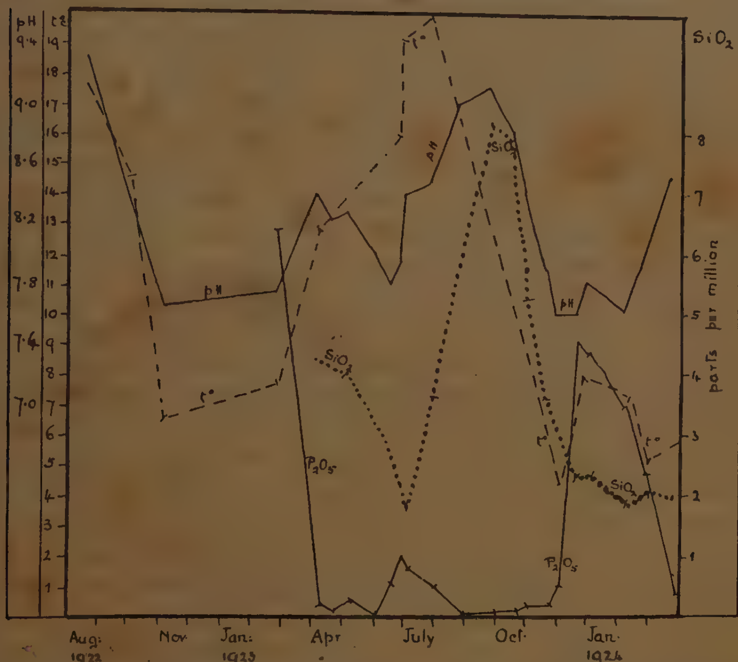

FIG. 35.—Seasonal changes in the water of Staddon Pond (after Atkins and Harris). The numerals indicating degrees of temperature also indicate phosphate, at 0·010 mg.P_2O_5 per litre.

These changes in solution-content of the water, as we see, are conditioned by the activity of plants, and partly also of animals; but the diminution in supply of food-salts reacts in its turn on the aquatic flora, and checks its multiplication, till decay restores the equilibrium and the cycle is complete. The quantity of life which any given water-body can support depends ultimately upon the supply of inorganic salts, and, according to the "Law of the Minimum," propounded by

Liebig, actually upon the supply of that particular food-material which is present in minimum relation to the demand. Minder, and some other continental workers, believe that the quantity of nitrates present is the factor limiting the development of life, at least in lakes of certain types, but some work done in this country seems to show that the supply of phosphates may be even more important. Of two ponds, studied by Atkins and Harris,[13] one had an inlet renewing the supply of dissolved phosphates, the other was without such, and in summer the phosphate-content remained at *nil* for a long period; after the vernal maximum in the latter, plant-growth declined rapidly and remained low throughout the summer, while in the other pond, with renewed phosphates, "masses of plankton-Algæ" were formed in summer; comparison of the nitrate-content afforded no explanation of the difference, which must apparently be attributed to the decisive factor of phosphate supply.

Along with all these changes in solution-content, and directly conditioned by certain of them, goes a marked seasonal and diurnal cycle of variation in electrical conductivity and acid or alkaline reaction, as measured in terms of hydrogen-ion concentration (pH value). The acidity of natural waters is usually due to the presence of dissolved carbon dioxide, and the pH curve for alkaline values is thus governed inversely by the curve for CO_2, acidity being least when the green plants are active in carbon-assimilation (compare Fig. 34).[15,16,9] Secular influences, especially the effect of alterations in temperature on the solution capacity of the water, may modify all these curves as drawn from actual records, but their trend in general is clear, and consistent in relation to the seasonal cycle, acting through the metabolic phases, so that the data may be unified into one harmonious conception, which, from the standpoint of the animal life, we may sketch as follows:

The general influence of seasonal changes in a temperate climate, by regulating plant-activities, ensures the repetition of marked phases in the chemical constitution of inland waters. The outburst of plant-activity which begins in early spring, when daylight strengthens, leads to a diminution in

the quantity of carbon dioxide present in the water and to an increase of oxygen precisely at the time when it is most needed for the respiration of the animals, which awaken to active life rather later than the plants. The nitrites, nitrates, phosphates, and lime-salts which in winter largely occur in free solution are during the summer combined by plant-activities into more complex substances, suitable for the nutrition of the animals, which, in the warmer months, are thus supplied with all the necessary oxygen and food to ensure their strong development and multiplication. The lower temperatures which set in with autumn first affect the animal life, which dies away or passes into resting-phases more fully and earlier in the season than the plants; the latter, like industrious handmaids, awaken earlier in the year, preparing in advance for the renewal of the active life of the aquatic fauna.

The inorganic salts dissolved in water certainly affect the fauna to some extent directly, as well as through the plants. The separate salts normally present seem to exercise each its individual influence upon animal physiology; excess of any may be hyper-tonic, or "toxic," in effect, while preservation of a due balance among the separate constituents maintains the organism in healthy condition, according to a modern theory, by "the principle of antagonism." Such a natural balance is found in normal sea-water, and removal of any one constituent cannot be compensated by addition of another, even though the resultant solution be made iso-tonic with the normal ([17, 18], and references therein). The proportions and "make-up" of the various salts are far more variable in inland waters, in most of which the total concentration is also very much less, as we have seen (Chapter I); yet it is probable that a due balance is none the less essential, and may be attained in different mixtures of the components. Certainly chemical neutrality is *not* the ideal; not only is such neutrality unlikely to occur in natural water, but it has been shown in certain cases ([19], and references therein) that distilled water at pH7·0 (the neutral point), even though it be perfectly pure, is fatal to some freshwater species. By common observation

animal life is richest in waters of slight alkalinity, and seldom occurs at all below *p*H4·7 or above *p*H8·5. These two points are regarded by Labbé [20] as biologically "critical"; *p*H4·7, the acid limit, is, as he points out, the iso-electrical point, at which the special properties of albumen are at their minimum development, while *p*H8·5, another turning-point in electrical influence, is that beyond which as a rule even the alkaline-loving salt-marsh species become extinct. It is difficult to disentangle the influence of an acid or an alkaline reaction *per se* from a specific action on the part of ions other than the H or OH, yet there is some evidence that certain organisms have their characteristic ranges in the scale of hydrogen-ion concentration. This has been demonstrated clearly for Molluscan types,[15] where the range varies from one species to another. Mosquito larvæ also seem to have their characteristic ranges: *Finlaya geniculata* and *Anopheles plumbeus* only develop satisfactorily in very acid water, at about *p*H4·4, and these two species are found in nature in holes in tree-stumps, where the water is always acid; species from normal habitats cannot endure a similarly acid range.[21] The case is complicated here by the attacks of *Saprolegnia*, a fungus which flourishes in acid water, but the importance of the *p*H in some way or other is very clear. The influence of too-acid water upon trout is deleterious,[22] and, passing to a tribe of very different affinities, certain Protozoa have their characteristic *p*H ranges.[23] Probably the limitation is imposed by some osmotic process: an alkaline solution tends to increase permeability of the organic membranes, while weak acids lessen permeability, stronger acids increase it again.[24] In pond-snails, which are killed by immersion in too-acid natural waters, death is preceded by the copious exudation of mucus, which quickly coagulates.[25] Wells has shown [26] that certain freshwater fishes, under experimental conditions, select slight alkalinity in preference to strict neutrality, and very slight acidity in preference to either; while Powers has demonstrated that fishes of various species have varying *p*H optima for the absorption of oxygen.[27]

As we have already remarked, it is often difficult to deter-

mine whether an apparent preference for particular hydrogen-ion concentrations may not be ultimately referable to some associated chemical factor. The *p*H of the water, though it varies within certain limits in every situation in relation to the quantity of dissolved carbon dioxide, is relatively fixed for each locality by the nature of the materials dissolved from the substratum. In chalk or limestone districts we find the extreme of " hardness " and alkalinity of the natural waters: *p*H values may be normally round about *p*H7·8, rising occasionally to 9·0 during the sunlight hours in weedy pools. Waters which flow over granitic rock or Palæozoic grits and shales have usually only very small quantities of lime or other salts in solution; they are " soft," and slightly acid in reaction, often with *p*H round about 6·4. In moorland waters, free from lime and on a peat substratum, the solution of vegetable acids (known roughly as " humic ") may bring the *p*H down as low as even 4·0; a usual figure is somewhere between 5·0 and 5·8. The scarcity of life in such acid waters (which we shall further discuss in Chapter IX) may be at least partially due to factors other than hydrogen-ion concentration as such: to deleterious influence on the part of humic acids, or to lime-starvation. In acid natural waters free from peat there is always a certain poverty of fauna, especially of Molluscan species, and in at least one soft-water district well known to the writer the freshwater types in general, Mollusca in particular, are not only few, but below the usual standards of individual size. We are reminded strongly of the small size and thin-shelled condition of freshwater Mollusca in general, as compared with marine (see Chapter I, p. 23), and it is probable that this special poverty is referable to special lime scarcity, intensified from the general condition. It is significant that in the Tropics, where high temperatures facilitate the physiological absorption of lime-salts, freshwater molluscs (especially *Ampullaria* and its allies) have shells of almost " marine " type in thickness and calcareous impregnation; remarkably thick shells are also formed by Gastropods living in Lake Tanganyika, where the percentage of salts of the alkaline earths, especially of magnesium, is high.

In the case of several isolated species the presence of lime-salts in the water appears to be a weighty factor in determining geographical distribution. *Gammarus pulex*, the freshwater shrimp, is recognised by European workers as especially characteristic of hard waters with a good percentage of calcareous matter and an alkaline reaction,[28] and observations made in British streams seem to support this view [15]; in the soft-water district just now referred to, this species, elsewhere so common, is restricted to a very small percentage of the streams, those with less acid reaction than the rest. Some species of *Planaria* seem to be particularly characteristic of hard waters, some of soft,[29] and in one British area where the distribution of pond-Mollusca has been carefully studied, *Limnæa* and *Pisidium* were found to dominate the hard and soft waters respectively.[30] *Pisidium* species are practically the only molluscs characteristic of some humus-waters.

The physical properties of the natural inland waters are no less important in relation to animal and plant life than the chemical. Reference has already been made to the influence of specific gravity of the water with regard to locomotion and support, and to the high importance of the surface-film in the lives of animals which live near it; some further discussion from a different standpoint is necessary. It is one of the peculiar features of water that its maximum density occurs at a temperature of about 4° C., whereas the freezing-point is 0° C. (for *pure* water only: the presence of dissolved material causes depression of the freezing-point); this feature is of high significance in relation to the powers of thermal conservation, already great in water, in virtue of its high specific heat and the latent heat set free in condensation and in freezing. The important consequence, from the biological standpoint, of this discrepancy between freezing-point and point of maximum density is that, when a body of water is sufficiently chilled, the heavier water, at about 4° C., tends to accumulate at the bottom, while the lighter water, at freezing-point, forms ice at the surface. Only long-continued freezing can solidify the whole mass, if it be beyond a few inches in depth, so that below the icy coating a body of free water is preserved in

which life can still be maintained at not too extreme a temperature; it is a common experience to see freshwater animals (*Cyclops*, *Dytiscus*, etc.) swimming actively beneath the surface of a frozen pond. (For discussion of the "thermocline" of deep lakes, see Chapter VIII.) This thermal conservatism of the fresh waters, though less pronounced than that of the ocean, is still great enough to cause their variations in temperature to lag far behind those of the atmosphere and of the land-surface, and we find as a rule less difference in species between the aquatic faunas of different climatic zones than between the sub-aërial. There are, nevertheless, certain species, or groups of species, known as "stenotherms," which can tolerate only a still narrower range of temperatures and must be limited in distribution to waters in which this range is not exceeded. Low-temperature stenotherms in all but Polar regions as a rule inhabit the depths of the great lakes or spring waters (see Chapters V, VI, and VIII) in which the temperature remains low throughout the year, though some are of seasonal occurrence in waters more exposed. High-temperature stenotherms are generally very limited in geographical range, or may occur in the neighbourhood of hot springs, in which latter case they generally have to encounter also certain peculiar chemical conditions (Chapter IX).

Another important physical property of the inland waters is their transparency—the extent to which they are penetrated by light. Whatever be the direct significance of light for animal activities (and there is a strong modern tendency to postulate a high importance in the general physiology, as well as the more obvious value in relation to vision), it has undoubtedly a very vital *in*direct significance, as conditioning the photosynthetic activities of green plants, which are, as we have seen, so fundamental in the economy of aquatic life in general.

A rough, but fairly accurate, measure of transparency is achieved by lowering a white disc of known diameter (Secchi's disc, diameter 20 cm.) and noting the depth of water at which it ceases to be visible. This depth must of course vary in relation to the intensity of sunlight, as conditioned by the

state of the atmosphere and position of the sun in the sky, which latter varies with the latitude, as well as with the season and time of day. Forel, the great Swiss limnologist, who first used these discs in freshwater work, found [31] that in Lake Geneva they disappeared at depths varying from 5·3 metres, in August, to 17·0 metres, the latter record being established at noon of a clear, cold day in March. The depth of disappearance is profoundly influenced by the turbidity of the water, which is of course affected by climatic factors (*e.g.* floods swelling the rivers, or the spring melting of glaciers), as well as by the quantity of organic life present in the water. Both factors are largely seasonal in any given water-body. With the clear waters of Lake Geneva, lying beneath a high sun, in a low latitude, may be contrasted those of Furesö, a Danish lake, in a high latitude and having a more abundant plankton; here a minimum penetration of 5 metres, a maximum of only 9 metres (in March), has been recorded, while in a flooded river, Spoon River, Illinois, the depth at one time recorded was so slight as 0·013 metre.[32]

It must not be supposed that such limits mark the final boundary of light penetration; by the method of lowering covered photographic plates and exposing them beneath the water the influence of actinic rays has been detected in Lake Geneva at 170 metres, in Walenstadt at 140 metres.[31] Below this, darkness is complete, and even much above it the light intensity is insufficient for photosynthesis by plants. Forel found the limit of abundant green vegetation in Lake Geneva at about 20 metres—a general level which seems to be fairly constant in such lakes. This is a level of profound significance, dividing the inland waters into two zones: a littoral zone above, in which a rich benthic fauna flourishes among abundant plants which supply it with oxygen and food in plenty, and a deeper zone, where life is more scanty, and special methods of obtaining food and air-supply must be adopted. (The deeper zone of lakes and its fauna are discussed in Chapter VIII.)

There is no doubt that light has, *per se*, a strong influence upon the movements of freshwater animals; many are "lucifuge," among which we number such benthic types as

hide under stones or burrow, to emerge at night; others, again, seem strongly "luciphile," at least when observed in an aquarium—such plankton-forms as small Cladocera (*Polyphemus*, *Bosmina* in particular) swim to the lighted side and crowd against it. But in such judgments discretion must be exercised, since more careful observations often show that the response varies considerably in relation both to the intensity of the light stimulus—many animals being positively phototropic to *weak* light, negatively to *strong*—and to contributing circumstances of quite other nature, such as oxygen-scarcity and hunger.[33, 34, 35] Strong light, such as is encountered quite at the surface on a sunny day, certainly has a repellent effect, other things being equal, on most, if not all, freshwater animals; the free-swimming plankton is never found quite at the surface, and frequently at some considerable depth below. (For movements of the plankton, see Chapter VII.)

The remarkable property by which water transmits pressure upon its surface equally in all directions is responsible for the existence of deep-water fauna. At a water-depth of only 20 metres, the pressure is twice as great as at the surface, and an animal living near the bottom of almost any large lake may have to support a pressure on each square inch of its surface of over 300 lbs.; such pressure can only be tolerated thanks to the pervading power of water, which transmits the pressure through all dimensions, eliminating the strain. Regnard[36] found that great pressure under water, artificially applied, caused tissues which had been stripped of their integument to swell by the induced imbibition of water; further, a pressure of 100 to 400 atmospheres, quickly applied, caused littoral animals to fall into a sluggish state from which they quickly emerged if the pressure were not maintained for long, but which would otherwise in time pass into death. Such pressures also inhibited the course of organic fermentation, the development of eggs of littoral fishes, and a number of other biological processes. The slackening of putrefactive processes may be of great significance for the maintenance of life at considerable depths, as checking the decay of food materials which drift down from the richer world above. It is probable that,

on the whole, the force of pressure in determining the limits of aquatic life has been greatly exaggerated, and that other factors must be called into account to explain the scantiness of life in deep inland waters—which, in any case, are none of them so deep, by a long way, as those abyssal pockets of the ocean in which life still maintains itself.

The sound-conducting properties of water are notoriously high, and it seems unreasonable to suppose that freshwater animals should not have taken advantage of this convenient factor for maintaining themselves *en rapport* with their surroundings. Many aquatic insects, as *Notonecta*, some Corixidæ and screech-beetles have stridulating organs of some power, which we may reasonably think are balanced by some sound-perceiving faculty; but, on the other hand, some organs, such as the otocysts of crayfishes, formerly believed, on the anthropomorphic interpretation of older naturalists, to function in the auditory sense, have now been proved by direct experiment to be purely concerned with static perception. Anglers tell us that fishes can hear acutely, but it seems certain on more orthodox authority that they have at least no tone-perception, though the "ear" is admirably adapted for perceiving vibrations of the water in a sense which approximates to "feeling" rather than "hearing." The special sense-organs of the lateral line, peculiar to fishes and some aquatic Amphibia, have certainly a static function and are also concerned in the perception of currents in moving water.[38] Next to the static sense, perhaps the most important and the most universally developed in aquatic life are those concerned with the perception of odour and contact. Aquatic beasts of prey swarm to the neighbourhood of food-material placed in the water: Voigt [37] has vividly described the rush of Turbellarians upstream, drawn by downstream-diffusing odours of the bait inserted for their capture, and such instances are common in the experience of every freshwater naturalist. Some fishes have the sense of taste located not only in the area about the mouth, but over a wider surface of the body: catfishes have taste-perceiving organs in the oral tentacles, with which they feel over the mud for tit-bits, but the Tom-

cod (*Microgadus*) has a still more curious type of arrangement. The taste-buds here are concentrated at the tips of the pelvic fins, which are filiform, and trail upon the bottom as the fish moves slowly along, "tasting" as it goes, and moving backward when a tempting morsel has been discerned, to seize it.[38] Such curious adaptations are only suitable to life in the aquatic medium; human city-dwellers may be sincerely thankful that this is so!

The tactile sense, of great importance to animals moving in the diffused light of the fresh waters, is everywhere highly developed, and its special instruments vary from tactile hairs and bristles, distributed over the body, to highly sensitive antennæ, thronged with bristles, such as we see in the Crustacea and some insect types. But this world of sense is one of which we know but little, and that little is often obscured in its interpretation by our own unconscious prejudice.

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CHAPTER IV

THE REPRODUCTION OF FRESHWATER ANIMALS

"You are to know, that there are so many sorts of flies, as there be of fruits . . . and their breeding is so various and wonderful that I might amaze myself, and tire you, in a relation of them. . . . Pliny hath an opinion that many flies have their birth, or breeding, from a dew that in the spring falls on the leaves of trees . . . and others say that Eels, being old, breed other Eels out of the corruption of their own age."—IZAAK WALTON.

A FULL account of the reproduction of freshwater animals might occupy many volumes; it must suffice, for present purposes, to focus attention upon certain aspects of the subject which bear special relation to the conditions imposed by the environment. It is convenient, in doing so, to divide the freshwater fauna into two classes, the first including animals which are aquatic throughout life, the second (mainly represented by insects) those which pass only their young stages in the water.

The former group at once challenge comparison with the marine fauna, and the special features which characterise their reproduction as compared with that of the latter are certainly related to the stronger influence of the seasons in the inland waters and to the prevalence of constant currents. The special tendencies in reproduction are: reduction of free-swimming larval stages, production of a relatively small number of large eggs, protection of eggs, long embryonic development, and presence of a marked seasonal rhythm.

Almost all groups of marine animals have their characteristic ciliated larvæ, often very delicate and helpless creatures, which drift among the plankton. Among the freshwater fauna, Copepoda and Phyllopoda with their nauplii, the very few sponges with their planulæ, and the small group of Polyzoa,

are outstanding exceptions to the general rule of direct development, leading to the emergence of young essentially like the adult in structure; and even these exceptional larval forms are usually found in or near the in-shore mud, not drifting freely in the plankton. Among Crustacea, the Cladocera (perhaps of all groups, the most perfectly adapted to life in inland waters), as well as Ostracoda and Malacostraca of fresh waters, have altogether lost the nauplius phase, and have direct development. The trochosphere larval phase of Annulata is eliminated from the life-history of freshwater Oligochætes and Hirudinea; the veliger phase of the Mollusca,

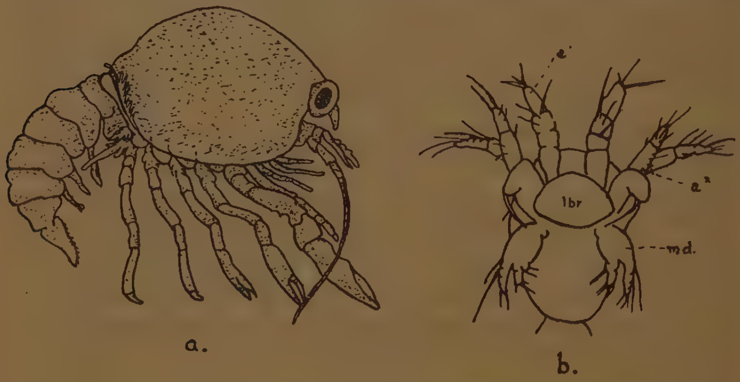

FIG. 36.—*a*, Young crayfish just after hatching; *b*, *Nauplius* of a Copepod (after Calman).

too, is almost gone. Freshwater Pulmonate Gastropods, like land snails, have lost it entirely; in the freshwater mussels there is, indeed, a corresponding phase in development, but it takes place within the shelter of the maternal gill-folds, and the young form which emerges into the outer world is an active, muscular "glochidium"—of which more later. The only freshwater mollusc which retains a free veliger phase is *Dreissensia*, already mentioned as a recent immigrant.

Direct development usually implies reduction in number of eggs and increase in individual size, since each must hold a store of yolk to nourish the embryo. A few instances will serve to show that many freshwater animals lay fewer eggs

than their marine relatives. Among Mollusca, the common oyster spawns something like 1,800,000 eggs at once; *Unio pictorum*, in fresh waters, has 220,000; *Anodonta cygnæa* has an exceptionally high figure for freshwater species, and may spawn up to 2,000,000, but as a rule the numbers of its eggs are round about 15,000. In Gastropods reduction is more noticeable: of marine littoral "snails," *Buccinum undatum* has 12,000 eggs, *Purpura lapillus* about 245 capsules, each containing 400 to 600 eggs; freshwater snails lay 20 to 100 apiece, the freshwater-limpet only 5 or 6, and the viviparous pond-snail about 15. In fishes the rule of reduction is general: to quote rather extreme examples, in the sea the haddock spawns 9 million eggs; the brook trout spawns 500 to 1000. *Cordylophora lacustris*, in salt water, bears a number of gonophores which contain usually from 6 to 12 eggs apiece; in fresh water the gonophores are fewer, and contain only 3 to 6 eggs in each. The prawn *Palæmonetes varians*, which in the marine littoral produces an average of 321 eggs, each about half a millimetre in diameter, lays in the inshore pools of lower salinity not more than 25 eggs, which are three times the size of those in the large clutches, and the embryos hatch out in a more advanced condition, and undergo fewer moults before they reach maturity.[1a]

Nearly all freshwater eggs are relatively large and heavy with yolk (except the summer eggs of Rotifers and Entomostraca, to be considered later), and so are "demersal," sinking to the bottom if left free. Some few plankton animals, especially among Entomostraca, produce small eggs, including oil-drops or air-spaces, which may act as floats, but these are seldom found freely floating, as they inevitably drift towards the shore and there find shelter.[2] The numerical reduction and prolongation of embryonic phases impose a strict necessity for protection of the eggs: in most species, the eggs are somehow anchored against the current in some sheltered spot;

FIG. 37.—Winter-egg of *Hydra* splitting its outer coat (from Bronn's *Tierreich*).

those which are shed loose have protective envelopes and can endure being buried in the mud, and often even desiccation.

The egg of *Hydra*, when released, is cased in a protective shell formed from the tissue which covered it in the maternal body; freshwater Turbellarians enclose their eggs in horny capsules which may be attached to stones or plants or lie between them in the mud; Oligochætes and Hirudinea form similar capsules. The worm-shaped leeches (*Hirudo*, *Aulostomum* . . .) glue the capsules firmly under sheltering stones, but the Clepsinidæ carry them attached to the broad bodies of the parents until the young emerge, and fix themselves temporarily by their suckers, now and then making short excursions

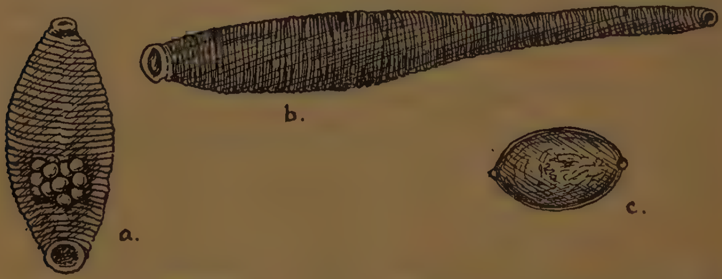

FIG. 38.—*a*, *Helobdella stagnalis*, a Clepsinid leech, sheltering the egg-cocoons (enlarged about 3 times); *b*, *Hæmopis sanguisuga* (*Aulostomum gulo*), a type of the strap-shaped Arhynchobdellid leeches (natural size); *c*, cocoon of *Herpobdella*, affixed to a stone (enlarged about 3 times).

from which they return at intervals to seek the maternal protection. Freshwater Pulmonate Gastropods coat the eggs with jelly, protective against mechanical shocks and the attacks of enemies, and commonly fix the whole mass upon some water-plant (e.g. *Limnæa*) or stone (e.g. *Ancylus*). In most freshwater Streptoneura (as *Vivipara*) the embryos develop to quite an advanced stage within the mantle cavity of the parent. Freshwater mussels shelter the young, as already described, within the gills; when the glochidia emerge they swim freely, flapping their valves, until they come in contact with the skin or (more often) gills of some freshwater fish; they fix themselves here, and the surrounding tissues grow, under the irritating stimulus, into a sort of cyst, which

protects the young intruders till they are ready for a less sheltered life.

Loricate Rotifers shelter their "summer eggs" within their sheaths, and some Bdelloids (as *Philodina*) even hatch them internally [3]: the "winter eggs," having no such maternal protection, are given thick resistant coats. All Entomostraca have thick-coated resting-eggs, and in many Cladocera a portion of the maternal carapace, the "ephippium," is shed off to enclose them still more securely; direct development of the summer eggs of Cladocera takes place in a brood-pouch dorsal to the mother's body, underneath the carapace; Copepoda shelter the eggs in egg-sacs borne on the abdomen (see Fig. 7, p. 34). Freshwater Amphipods and Isopods shelter eggs and embryos in a thoracic brood-pouch formed by the

FIG. 39.—Glochidium larva of a pond-mussel (much enlarged); *b*, byssus-thread.

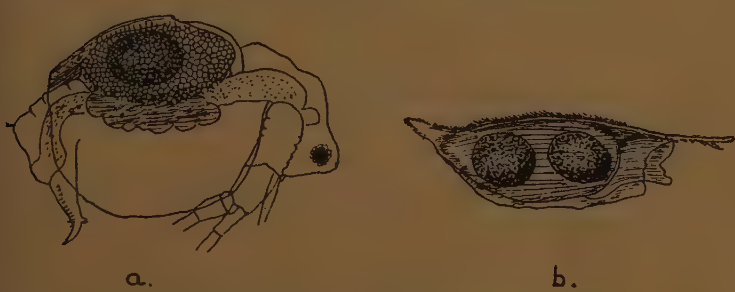

FIG. 40.—*a*, *Moina rectirostris*, ♀, with ephippial thickening and one winter-egg; *b*, cast ephippium of a *Daphnia*, with two winter-eggs (after Welldon).

development of scaly "oöstegites" on the limb-bases. The crayfish eggs are glued to the abdominal appendages, and hatch into miniature adults which for a time cling on by their pincers. Hydrachnidæ (water-mites) fasten their eggs to plants

by jelly-masses (as *Eylaïs*), place them in holes bored for them in plant-tissues (as *Hydrarachna*), or under stones (as *Sperchon*), or even within the gills of mussels or the chambers of sponges (as *Unionicola*).[5]

Salmon and trout, bullheads, grayling, and minnows lay their heavy demersal eggs among stones or gravel, to which their jelly coats often adhere; the perch and all Cyprinidæ deposit them among plant-growth, sometimes in gelatinous masses, sometimes in sticky beaded strings, that fix themselves among the plants.[6, 7] One little fish, the bitterling

FIG. 41.—A female *Gammarus*. The position of the eggs in the thoracic brood-pouch, sheltered by the coxal plates, is dotted in (partly after Sars).

(*Rhodeus amarus*) of North Germany, takes it upon itself to deal out retribution to the freshwater mussels for their use of fishes as their nurses: the female fish, with her long ovipositor, inserts her eggs into the mantle cavity of *Anodonta* or *Unio*, where they develop.[8] Perhaps the most familiar example of care for the young in fishes is the stickleback, with its nest of weeds woven by the male, who keeps guard until the eggs are hatched; but is by no means a unique instance among freshwater fishes. The North American bow-fin (*Amia calva*) is no less devoted to his offspring (N.B. " his ": the male parent is nearly always the responsible one among fishes): not only does he guard the eggs within his reedy nest, and

flap his fins to make oxygenating currents over them, but he even plays nurse and tutor to the young for several weeks after they are hatched. The male *Protopterus*, in West African swamps, digs a hole in the mud to serve as nest, and aërates the eggs by waving his tail. *Lepidosiren*, in the River Paraguay, makes a complicated "nest" with a tunnelled passage, and stays on guard, developing strange gill-like fringes on his hinder fins which may assist in his own respiration or even in transference of gases to the water around the eggs. Several catfishes in America (Siluridæ) also make nests, and the bubble-fishes (Osphromenidæ) of the Malay Islands buoy up their floating domes of weed with bubbles blown into them from below. The eggs, laid at the bottom, float or are blown up to develop at the surface under these domes, and the father is continually on the watch to blow up developing eggs if they sink down. This looks like a most beautiful example of fatherly devotion, but, alas for sentiment! when the young fishes emerge, both parents chase them and devour as many as they can catch,[9] a fact which illustrates very well the limitations of instinctive conduct. The Cichlidæ (freshwater wrasses), of Southern rivers, have the most peculiar of all methods of protecting their eggs, which they hold at the back of the throat, just near the openings between the gills; the eggs are thus assured of aëration and of protection from enemies and currents, though the position may have its own perils, leading in some cases to infanticide.

The influence of the seasons upon reproductive cycles in fresh waters is profound. Spring is the season for egg-laying in the majority of the freshwater tribes, and the young develop in the season of mild conditions and plentiful food-supply which follows. Some of the lower animals avail themselves of the summer's opportunities of rapid development in signal fashion: *Hydra* forms vegetative buds which break off to lead a free existence, *Cordylophora*, sponges and Polyzoa extend their colonies by rapid vegetative growth; many freshwater Turbellarians, and even some Oligochætes (e.g. *Naïs*), multiply during the summer by transverse fission, cutting off buds from the posterior end of the body; Entomostraca and

Rotifera lay summer eggs which develop rapidly, running through many generations.

With the approach of winter, temperatures fall and food becomes more scarce; many of the lower animals die off altogether, and leave behind them enduring reproductive-bodies, as a rule hard-coated and well-stored with food. Sponges disintegrate and free the "gemmules" which have been formed within their tissues: these are bodies asexually formed by the fusion of amœbocytes, around which groups of spicules aggregate; the triple-coated gemmules can endure

FIG. 42.—*a*, Portion of a colony of *Plumatella*, showing statoblasts (*st.*) developing on the funicle; *b*, a statoblast of *Cristatella mucedo* (actual diameter, 1 mm.); *h*, hooklets; *f*, flotation-girdle of air-cells.

even desiccation, and rest through the winter, germinating in spring. *Hydra* has its resistant winter eggs. Nearly all freshwater Polyzoa (all Phylactolæmata) form winter bodies known as "statoblasts," most like sponge-gemmules, but differentiated from the funicle between the zoöid and the common stem of the colony. These have strong coats, often with air-inclusions, by which they float until they drift to shore and become entangled (often by special hooklets) among the plant-stems, and so await the spring. Drought and frost cannot hurt them; indeed, in some cases exposure to severe conditions seems a necessary preliminary to their germination. *Paludicella*, the one freshwater Polyzoan of the Ectoprocta,

produces "winter buds," externally formed, in place of statoblasts; these sink and lie buried in the mud till spring. Smaller Crustacea and Rotifera no longer lay their quickly-hatching eggs; the "winter eggs" have strong, thick, outer coats, and are heavy with yolk, and do not germinate at once.

But the complicated reproductive cycles of these last-mentioned groups require more careful separate consideration. The phenomenon of "cyclic reproduction" in Cladocera was long believed to follow a straightforward course in direct relation to the seasons. At certain times of year, only females are found, and these produce a large number of eggs which do not require to be fertilised, but develop parthenogenetically and very rapidly, each absorbing three of the neighbouring cells in the ovary, and feeding on their substance. They are then extruded into the brood-pouch already mentioned, which is well supplied with blood-vessels, so that some nourishment may pass into the pouch to supply the embryos, which are here retained until fully developed, and even, in some Daphnidæ, until so far mature as to form parthenogenetic eggs themselves. As many as twenty or thirty of these eggs—or sometimes even more—may be comprised in a single brood, and broods may be produced at a very few days' interval, so that multiplication in this phase is exceedingly rapid. After a number of these generations, all giving rise to parthenogenetic females alone, some members of the last broods of the season develop into males, which fertilise the eggs of females, and a new phase sets in. The eggs thus to be fertilised are already distinguished from their predecessors: each, while within the ovary, has absorbed the contents of a great many surrounding cells, and its cytoplasm has become heavily laden with dark yolk-granules. As a rule, only one egg in each ovary comes to maturity; it is then passed out and fertilised in the brood-pouch, after which either a thick chitinous or gelatinous coat is formed about it before its extrusion (*Sida*, *Polyphemus*, *Leptodora* . . .) or, more usually, a portion of the maternal cuticle, shed off on moulting, remains wrapped about it as a protective envelope. In many of the Daphnidæ this portion of the carapace is strongly thickened before the moult into a

definite saddle-shaped "ephippium" (see Fig. 40): in such cases there are never more than two resting-eggs. Although the fertilised egg, when thus set free, has already undergone a little segmentation, a fairly long period of quiescence always intervenes before final development and hatching, and it is in this form that members of many species survive the winter. Indeed, for many years the life-cycle of all Cladocera was believed to comprise only the following phases: summer parthenogenesis by a number of generations of "summer eggs" producing only females, autumn production of males and fertilisation of "winter eggs," winter rest in the quiescent egg, and spring germination to restart the cycle.

But the investigations of Weismann [10] showed that the matter was not quite so simple; these "winter eggs" are not always produced in autumn, but many species form them in early summer, and Weismann substituted for the misleading terms "winter-" and "summer-eggs" those of "Subitaneier" and "Dauereier"—quickly-developing and resting-eggs. He further found that the annual reproductive cycle was not alike in all Cladocera: certain species, especially among the Daphnidæ, are di- or polycyclic, *i.e.* have two or more sexual phases in the year, one of which always occurs towards autumn, another usually about May. Others (e.g. *Polyphemus*) are monocyclic, having only one sexual phase in the year, while there are instances of species in lake-plankton which seem to be parthenogenetic only: such are said to be acyclic. Polycycly, with its several series of resting-eggs, is specially characteristic of forms (e.g. *Moina*) which live in small ponds, liable to desiccation; acycly often distinguishes the plankton-types. This seems to point to adaptation of the cycle to external conditions, but Weismann was nevertheless strongly of opinion that the cycle of each species was fixed by an interior biological rhythm which outer circumstances could not alter.

Recent discoveries have tended on the whole towards a modification of this view; but before discussing them we must mention Hertwig's suggestion,[11] that the repetition of parthenogenetic phases entails a progressive disturbance

of the biological balance between nuclear and cytoplasmic relations, which must be restored by the formation of the male sexual cell.

Certain facts observed in nature seem to tell in favour of an influence on the part of external circumstances: for example, a particular species may be alternatively mono- and polycyclic under different conditions. Zschokke records [12] that common *Bosmina* and *Chydorus* species, which in the European plains are di- or polycyclic, or even sometimes acyclic, become strictly monocyclic in high Alpine lakes. Ekman [13] has added the discovery that monocycly is also characteristic of these same species (as, indeed, of Cladocera in general) in lakes and ponds in the far North. Ekman drew the obvious inference that polycycly came in as a modification owing to the longer opportunities afforded for multiplication in the full summer of the plains. Another fact which seems to tell against the theory of an innate rhythm leading to the production of males after a fixed number of generations is that even in the sexual generations a few parthenogenetic females quite frequently occur.[14] Again, parthenogenetic females which survive the winter sometimes begin in spring by giving birth to quite a number of asexual generations, then form the sexual at the same time as that of their production from individuals newly hatched in spring.[15]

Nevertheless, the observations of several workers, especially those of Papanikolau,[21a] show that amongst the progeny of a single individual, developed from a winter egg, the tendency to bisexuality increases with the number of generations. On the other hand, experimental evidence [16, 17, 21a] has shown that the sex-ratio may be influenced by outside circumstances: cold, hunger, and the presence of metabolic waste-products in the culture-water raise the tendency to production of males. Probably the safe conclusion is that of Keilhack,[22] that each race has its maximum number of parthenogenetic generations fixed, but that unfavourable circumstances may cut short the normal cycle. We need still more careful records of the generation-cycles in nature, especially in small ponds, and in tropical regions where temperature is pretty even. In

any case, in our own temperate climate, the usual autumn formation of resting-eggs coincides most felicitously with the onset of severe weather conditions and scarcity of food, while the polycycly of pond-species, whatever be its origin, is no less felicitous in relation to recurrence of summer droughts. We must, however, note that resting-stages are frequently interpolated between the union of two gametes and subsequent development of their product, in organisms of very varied types, and quite without relation to external conditions, *e.g.* in many Rhizopod Protozoa, and in *Ceratium*, a Dinoflagellate.[23]

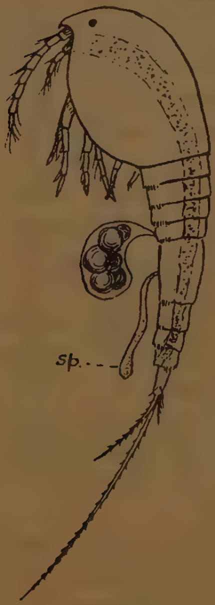

FIG. 43.—A female *Canthocamptus* with egg-sac and spermatophore (*sp.*) of the male still attached.

The reproduction of Copepoda is always sexual; after copulation, in which the modified antenna of the male is used as clasper, one or two spermatophores remain upon the body of the female, and may serve for several successive clutches of eggs.[24] Resting-eggs are always formed at some time of the year, and some species certainly form quickly-developing eggs as well, although the cycles have not been thoroughly investigated throughout the group. According to Wolf,[25] there are perennial forms (all di- or polycyclic), summer forms, dying off in autumn (usually monocyclic, especially in lakes), and winter forms, which live beneath the ice (mono- or dicyclic); but one species, e.g. *Cyclops strenuus*, may range itself in different classes in separate habitats. Such observations seem to support the view that the cycle is to some extent dependent on the action of external influences.

In the Phyllopoda [25, 14] the cycle is not at all rigidly fixed, and in some species parthenogenesis seems to be capable of indefinite duration. *Apus* and *Limnadia* produce only resting-eggs, which may or may not be fertilised: males are very seldom

seen; *Artemia* forms both latent and quickly-developing eggs, irrespective of fertilisation, and only in *Branchipus* fertilisation seems to be always a *sine quâ non*. Freshwater Ostracoda seem to be mainly or entirely parthenogenetic.[14, 25]

Rotifera also have two kinds of eggs, the latent eggs very thick-walled and resistant, and species found in small ponds (as *Brachionus angularis*) tend to polycycly, while in larger lakes monocyclic "summer-forms" are more usual.[26] The males are very small, and those of some species have never been seen: the quickly-developing eggs at least are parthenogenetically formed. Krätschmar's observations on *Anuræa valga* seem to point to a progressive degeneration consequent on rapid multiplication by parthenogenesis as the factor in determining the incidence of a sexual phase[27]; but, on the other hand, there is strong evidence[28] of the important part played by nutritional factors; as we have seen, the maximum and minimum development attend closely upon the presence of abundant Algal plankton and its decline.

The life-histories of those animals which spend only a portion of their life in water—chiefly Amphibia and insects—usually bear a close relation to the cycle of the seasons. In all these the aquatic phase occurs early in life; the eggs are laid on or near water, in which they hatch into a larval phase of active feeding and rapid growth succeeded by some sort of metamorphosis which leads to the adult reproductive phase passed on dry land or in air. It is true that many Amphibia are to some extent dependent on water all through life, but in all of them, as in all "aquatic" insects, the definitely aquatic phase is that during which the greatest growth occurs: a significant fact, which leads one to speculate upon the reasons for this choice of breeding-place, especially by the insects, in whose case there is no direct hereditary tie. An obvious advantage of water over dry land as a breeding-place lies in its fluidity, which renders a hard coating over the egg unnecessary; but insects as a class have solved the problem of protection of the eggs on land, and the large numbers of eggs still produced by aquatic layers evinces a certain precariousness as to their fate which tells against a theory that

the habit has survived because of any security conferred upon the eggs. Probably the advantage of aquatic surroundings is chiefly operative during the larval phase: seasonal changes in temperature are less marked in water than on land, and, more important still, aquatic plant-growth never quite dies down, and some organic detritus is always available, so that in water there is never that extreme food-scarcity which may prevail on land in winter. This is particularly important for young, growing creatures. It is significant that almost all insects with aquatic larvæ pass the winter in the larval phase (with a very few exceptions, as some gnats and beetles): it may well be that their aquatic breeding-habit owes its survival in so many odd families of insects to this escape from the severity of winters on land. In most cases, the winged reproductive phase is still retained, though shortened in many: it provides the best means of distributing eggs more widely, avoiding overcrowding in particular localities and extending the geographical bounds of the species.

But aquatic egg-laying carries with it certain disadvantages, especially for insects of the higher orders, whose life-history includes two separate phases of helplessness, the pupal phase as well as that of the egg. Not only is the problem of protection (especially against drifting currents) to be faced twice over in such lives, but also there remains the difficulty of contriving the emergence of a winged aërial creature from underneath the water. The several orders of aquatic insects show accommodations of such varied types to these necessities that they must receive separate consideration in two series, the hemi- and the holometabolic.

In hemimetabolic insects metamorphosis does not involve a helpless pupa-phase, but proceeds gradually through a long series of moults, so that the older larvæ, or "nymphs," have all the organs of the adults, even the wings, though these are not yet inflated with air, but folded in skin-pouches. For such, the change of medium involves less serious difficulties than for holometabolic types.

The *Hemiptera* or *Rhynchota* (including water-boatmen, pond-skaters, etc.) have, indeed, found aquatic or semi-

aquatic life so congenial that some of them seem on the way to abandoning the habit of flight entirely, although many still indulge in nocturnal flights, especially at mating. Quite commonly, separate individuals of the same species may have fully-formed wings, rudimentary wings, or no trace of wings at all: a case of polymorphism which is probably evidence of retrogressive evolution. All aquatic Hemiptera attach their eggs to plants for safety, usually fastening them down by some sticky secretion; but water-scorpions (*Nepa*) use their long, sharp ovipositors to bore into floating leaves, and then insert the eggs, the head-ends with their fringe of respiratory filaments projecting. There is, of course, no problem of emergence to be faced, as all the adult forms are uninjured by submergence (see Chapter II, p. 53). Spring is, as usual, the egg-laying season.

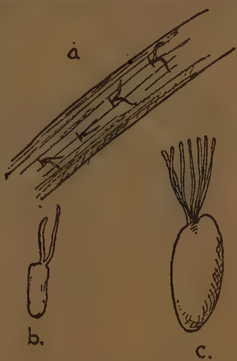

FIG. 44.—*a*, Piece of reed, with eggs of *Ranatra*, their respiratory filaments projecting; *b*, single egg of *Ranatra*; *c*, single egg of *Nepa* (*b* and *c*, enlarged about 10 times).

Plecoptera (Stoneflies) have four perfect wings in the imago, and fly heavily near water, or cling to bushes over rapid, stony brooks, near which they mate. The largish, heavy eggs cohere in masses, and are dropped into the water by the females, which fly or run above it. Imbibition of water causes the eggs to swell, and by the solution of a binding slimy fluid they fall apart. and the current rolls them under stones to which they cling, in some cases, by filaments or mushroom-shaped and clustered adhesive knobs.[29] The larvæ, which cling to the stones, are known by their two jointed caudal-filaments and two-clawed feet: larger forms have tufts of filamentous gills at the limb-bases, smaller forms have none. Egg-laying takes place between early spring and summer, according to the species; the larvæ hatch out by autumn and live through at least one winter (probably two, in some species: careful records are needed here) on a carnivorous diet. At last the full-grown nymph creeps out of the water, and emergence takes place in the

shelter of some stone. So soon as the first split appears in the back of the thorax, air passes into the spiracles and inflates the tracheal tubes, swelling the body within, expanding the wings, and hastening complete emergence. Last, holding to the stone by its fore-feet, the creature carefully withdraws its delicate tail-filaments from their sheaths (in larger stoneflies: some small species have them reduced to stumps), and in a few hours flight is possible.

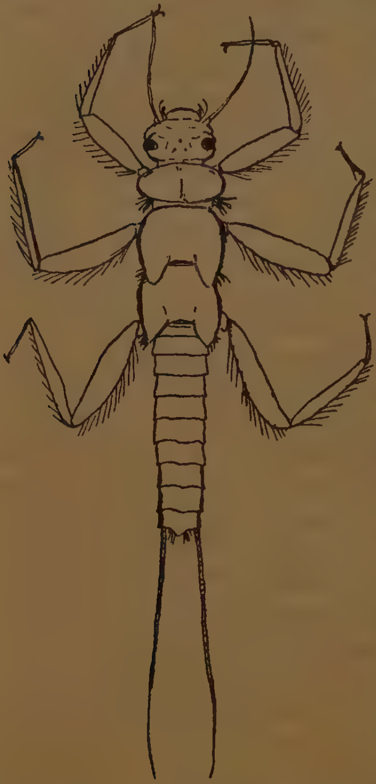

FIG. 45.—Nymph of *Perla cephalotes*, from a swift stream. Actual length, 1½ ins. The abdominal segments are slightly flattened ventrally; the dorso-lateral flanges of head-shield and thoracic segments, and the fringed and flattened femora, are pressed closely against the stone under which the animal clings. Note the gill-tufts on thorax (near the coxæ) and on last abdominal segment.

The case of Ephemeridæ (mayflies) is similar in general; the heavy eggs often adhere to the bottom by a gelatinous envelope, or in some species there may be anchoring threads or knobs. *Baëtis* enters the brook for oviposition, fixing the eggs one by one in parallel rows which form an oval patch on the under-surface of a stone.[29] Here, again, the winged nymph comes out of the water (sometimes balances on the surface-film) for the moult, but in this case the creature which emerges is only a "sub-imago," usually a sluggish insect, like the adult in form, but dull in colour: this must moult again on land, usually within about twenty-four hours of its own emergence. Large species have a larval period of two years' duration; small ones may have

only one, but even this is very long indeed compared with adult life, which in many species lasts only a few hours, and in none long enough for food to be required: the phase is wholly reproductive. Emergence takes place throughout the summer, the date varying with the species; a special

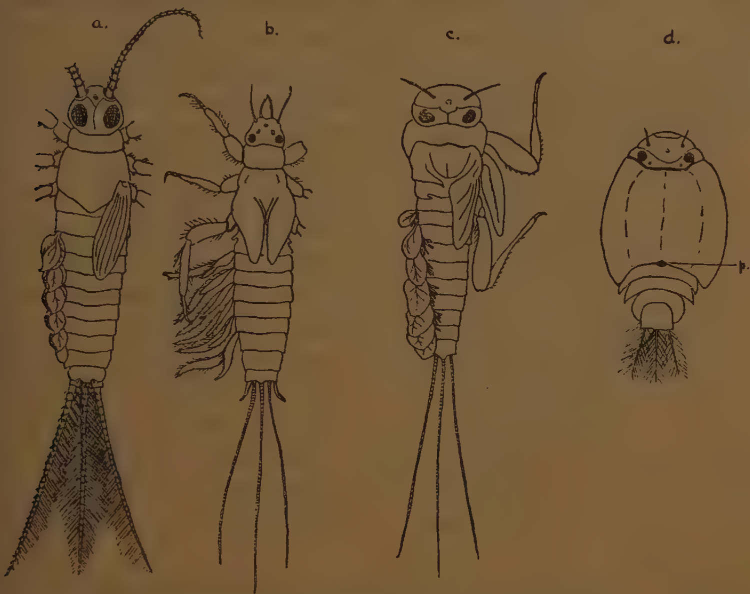

FIG. 45A.—Nymphs of some Ephemeridæ (after Vayssière). *a, Clœopsis,* a swimming type with cylindrical body and fringed tail-filaments; *b, Polymitarcys,* a burrowing type with strong digging-limbs; *c, Heptagenia,* a stone-clinging type with broad, flat head and thorax; *d, Prosopistoma,* extreme development of the burrowing type; *p,* aperture leading to the over-arched gill-chamber. (The wings and gills are shown on one side of the body only, in *a–c*).

feature is the simultaneous emergence of vast crowds of individuals of a single species, all within a few hours or a day or so, along one stretch of water. Many naturalists have observed these swarms, but none has described them so beautifully as Réaumur, in his account of the swarming of *Polymitarcys* from the Seine and of the fate which overtakes the mayflies when once their racial duty is fulfilled. These larvæ are much like those of stoneflies, but they have usually

three caudal-filaments in place of the two which distinguish the latter, also the tracheal gills are borne on the abdominal segments. There is much variation in form and habit between the species: some burrow in river-banks, and have strong fore-legs for digging, and fringed, branching gills (as *Palingenia* and *Ephemera*); some shelter under stones, and have flat bodies and plate-like gill-covers (as *Ecdyurus* and *Heptagenia*). The swimming-nymphs (as *Chlœon*) have weak legs and fringed tail-filaments; *Baëtis*, which clambers among mossy stones, has a body like that of a swimming type, with strong hooked claws.[30]

The last of those orders in which the nymph, with wings already formed, comes out of the water for the final moult, is that of *Odonata* (dragon-flies). Here, the period of adult life is longer, and the swiftly darting dragon-flies pursue small insects on the wing, and feed on them, but the adults do not survive the winter, whereas the larvæ winter in the ponds and slow streams. The larvæ are very varied in form (see Chapter II, p. 44), but all may be recognised by the enormously developed labium, which is armed with grasping hooks and can be shot out like an arm to seize the prey. Most dragon-flies affix their eggs to plants at the water-surface, or even plunge below to puncture stems and leaves for their insertion, and this attention has its converse in the effort which the nymph exerts to climb up by some plant to moult in the dry air. Tennyson's perfect account of the emergence of the dragon-fly is too familiar to need quotation here.

Among the holometabolic insects the small group of *Neuroptera* includes some types with aquatic larvæ. In *Sialis* (the alder-fly) the larva is aquatic, breathing by tracheal gills, but can endure exposure to moist air—fortunately for itself, since the arrangements for its survival seem very incomplete. The eggs are generally deposited in patches on leaves or bare earth somewhere near the water, and the first task of the larva, on hatching, is to find its way into some pond or stream. It lives a full year, burrowing in mud or gravel, and then sets out upon another journey, leaving the water to scoop a hollow in moist earth for its pupation, which occupies some months.

The imago feeds on other insects, but does not last out the winter: this is a perfect instance of the way in which so often responsibility for all the difficult crises of life devolves upon the larva. Little is known in detail of the life-histories of other Neuroptera, but we must mention the Spongilla-fly (*Sisyra*), whose small larvæ shelter in freshwater sponges and feed upon their juices.

Many *Coleoptera* frequent the inland waters, and in many

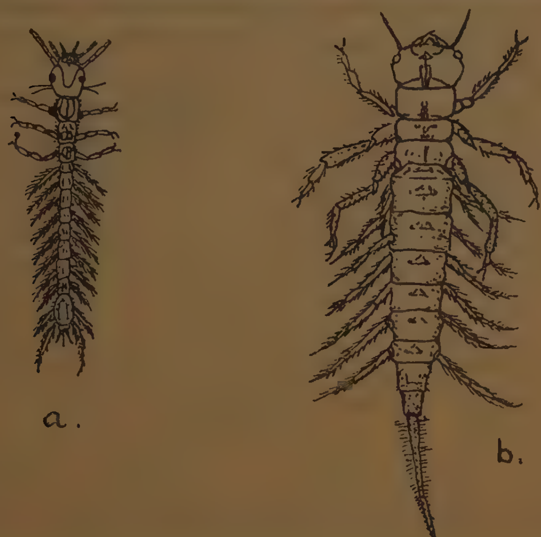

FIG. 46.—*a*, Larva of *Gyrinus*; *b*, larva of *Sialis*. Each has strikingly well-developed abdominal tracheal-gills. (Both about twice natural size.)

of them the adults can stand submergence (see Chapter II): some are even strong swimmers. This greatly simplifies the engineering of the life-crises, just as in Hemiptera, though here there is the pupal phase to be protected. Most water-beetles fasten their eggs to plants: it seems to be the duty of aquatic plants not only to make bare existence possible for the animals, as we have seen they do, but also to come to their rescue at every crisis in their lives. *Dytiscus* bores holes for the eggs in plant-tissues, like the water-scorpion, and many swimming beetles follow this rule; but some Hydrophilids make beautiful

floating cocoons of silk, holding about a hundred eggs, and moor them up to some surface-growing plant. Most beetle-larvæ are of the same general type as those of ground-beetles, with cylindrical bodies, strong mandibles, and well-developed legs, and breathe air at the surface, though *Gyrinus* and a few others have tracheal gills. The water-pennies, larvæ of some brook-beetles (*Psephenus*), are limpet-like in outline, as the segments are produced into broad, overlapping flanges, which are pressed closely against the stones in rapid streams. Most beetle-larvæ seem to live only a single season, and pupate in

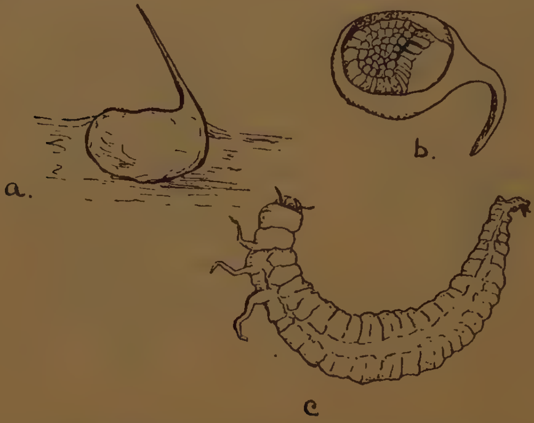

FIG. 47.—*a*, Floating egg-cocoon of *Hydrophilus piceus* ; *b*, the cocoon opened, to show the eggs ; *c*, the larva. (Partly after Miall.)

autumn, scooping burrows in the moist earth of the banks. Some of the pupæ (*e.g.* in *Hydrobius* and *Hydrophilus*) have spines or hooks upon the body which support them above the floor of the burrow or suspend them from its roof—a beautiful device to shield them from injurious pressure. Pupation lasts the winter, or, at least, the adult does not emerge until spring. *Donacia*, true to its phytophilous habit, does not pupate in soil, but in a cocoon fixed to the submerged roots of its food-plant. In Coleoptera we see a great reversal of the usual course of events, for the imago is the long-lived and " responsible " phase : we note that it is in these cases at least semi-aquatic.

In the *Trichoptera* (caddis-flies) the hairy-winged adults are short-lived, and never fly far from brooks. The eggs are laid in jelly-masses near the water, into which rain-showers wash them down, and they adhere to stones or leaves. The larvæ are truly aquatic, and the larger forms breathe by tracheal gills, which are kept stirring by the movement of the water in wandering and net-spinning types (Rhyacophilidæ, Polycentropidæ . . .); case-forming Limnophilidæ, Phryganeidæ, etc., always have an open pore or larger orifice at the posterior end of the tube, and keep a current moving through the tube by undulating movements of the body. The varieties in form of body, and especially of case, are almost infinite: cases may be made of sand, pebbles, leaves, bark, and even adorned with snails and other caddises; in form they may be tubular, four-sided, hornlike, flattened—some special types will receive mention in connection with their habitat. A distinctive feature of all caddis-larvæ is the possession of two curved posterior abdominal hooks, set in papillæ or on jointed bases on the last body-segment. Pupation is very well provided for: it takes place under water, and in case-bearing caddises the case is strengthened and closed by silken gratings or small pebbles and either partially buried in mud or carefully wedged and fastened among stones (*Mesophylax*). Silk-spinning larvæ construct tubes of stronger build than the loose mesh previously made, and wandering Rhyacophilidæ and *Hydropsyche* build roomy huts of small pebbles fastened on to larger stones. In many species the pupa develops a strong crossed "beak" formed from the mandibles, a transitory organ used to break open the case. Pupation lasts through winter; in spring the pupa breaks out

FIG. 48.—Larvæ of Trichoptera. *a*, campodeiform larva of a wandering hunter; *b*, grub-like larva of *Limnophilus*, a case builder.

and seeks the water-surface, swimming actively in many cases, floating up in others, and pushes through the surface-film, so that the adult emerges into dry air, and can flutter away from the cast skin when its wings are dried, or balance on it till wind or current drive the raft to shore.

The last and most highly-evolved order of insects in which aquatic larvæ are at all common is that of *Diptera* (the true two-winged flies). It is difficult to give any comprehensive account of the very various modifications connected with aquatic breeding in this group, but we may trace certain general principles in connection with egg-laying and emergence. In running water, the eggs are generally laid, like those of Trichoptera, in gelatinous masses which adhere to solid bodies, but in still waters there is some variety of method. Sometimes, as in *Chironomus* and *Tanypus*, the eggs are enclosed in strands or circular masses of jelly, which float on the surface and later attach themselves to solid bodies; sometimes, as in *Eristalis*, they sink separately to the bottom; sometimes, as in the gnats, they are buoyed up by little air-sacs, either singly (*Anopheles*) or in masses like rafts (*Culex*). Eggs which are thus floated are those from which will emerge delicate larvæ,

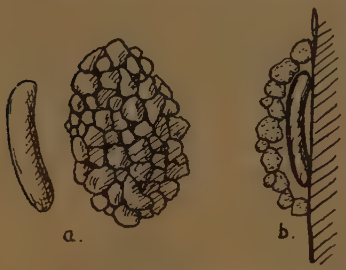

FIG. 49.—Pupa-house of *Rhyacophila*. *a*, House and cocoon removed from it; *b*, diagrammatic section of cocoon attached to a stone.

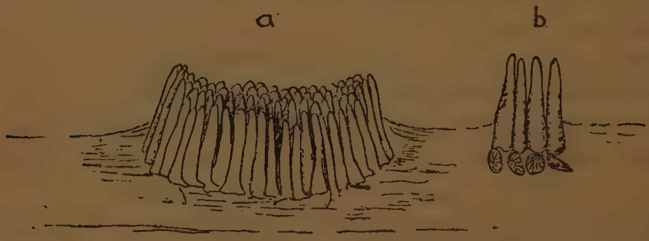

FIG. 50.—*a*, Egg-raft of *Culex*; *b*, eggs after hatching (after Lulham).

hanging from the surface-film: those which produce mud-living larvæ are allowed to sink. The floating larvæ in still waters usually form fairly active pupæ, which also hang from the film by respiratory tubules, but thoracic, not abdominal, as in the larvæ, and the imago rests on the old pupa-skin till it can fly away or is drifted to the shore, as in Trichoptera. The worm-like larvæ of *Dicranota* and many Limnobiidæ have bottom-living pupæ, which wriggle out along the mud, using

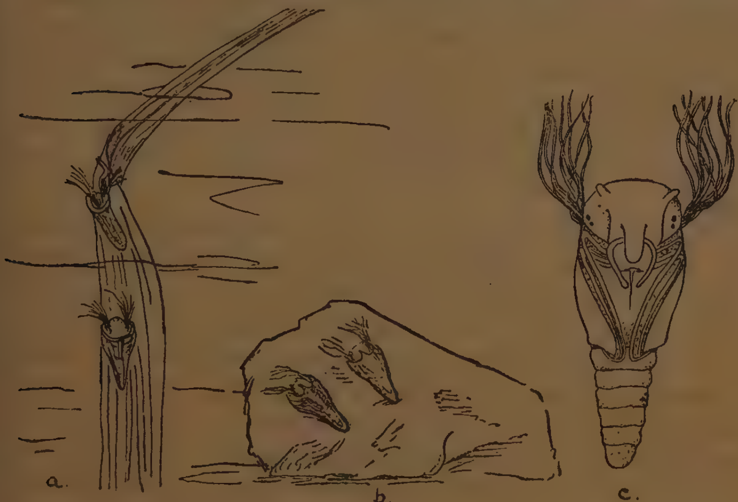

FIG. 51.—*Simulium* pupæ. *a*, *b*, Pupæ of *S. reptans* and *S. latipes*, in their shield-shaped cocoons, attached to weed and stone; *c*, a single pupa of *S. reptans*, removed from the cocoon, showing the four two-branched respiratory filaments on each side.

ventral thoracic spines and stumpy paired abdominal processes in gripping the substratum; a few, like the rat-tailed maggot (*Eristalis*), which lives in foul and stagnant water, wriggle out to pupate in loose soil. In *Eristalis* the larval skin forms a hard, almost woody case around the pupa, retaining the respiratory "tail," although two pairs of additional horn-like breathing-tubes develop on the head; after a week or two, the head end of the case is pushed off, and the fly emerges. The most familiar Dipteran larva in rapid waters is that of *Simulium*, the sandfly, which has already been described

(Chapter II, p. 40—also see VI). Pupation in swift waters is a dangerous business, and this larva spins an extra shield-shaped pocket, which is glued well down to a stone or weed. In this the pupa rests, its head upstream, at first enclosed in an oval cocoon, through which in a short time two bunches of respiratory filaments spread into the water, sprouting from the neck of the pupa. The emergence of the fly is a beautiful instance of adaptive mechanism: for about a fortnight previous to this crisis, a bubble of air extracted from solution gradually accumulates beneath the pupal skin, distending it further and further, until at last it bursts, and the winged insect is shot up to the surface on the bubble. Being very light, and saved from wetting by a hairy coat, it runs over the water-film, or quietly spreads its wings and sails before the wind.[31]

Very few members of any other insect orders are aquatic, but we must mention a few Hymenoptera, e.g. *Agriotypus*, in which the females venture just into the water to deposit their eggs under the skins of caddis-worms, puncturing them in the manner of an ichneumon. The larvæ live and grow here, until their victims reach the helpless pupa-phase, during which they finally devour them, and undergo their own transformation within the cases of the murdered hosts.[32] *Polynema* and *Prestwichia*, two small Hymenoptera whose larvæ parasitise water-insects, actually spend much of the adult phase in shallow pools, where *Polynema* swims with oar-like motions of the wings, *Prestwichia* with its long hind-legs, keeping the wings folded.[33, 34]

A very few Lepidoptera also have larvæ which develop from eggs laid against floating leaves by moths which run about the surface-film; these larvæ spin silken shelters on the leaves and usually stay at the surface, though the *Paraponyx* caterpillar has filamentous tracheal gills, and can live submerged.

The life-cycle of common frogs and toads needs no description here: it illustrates almost diagrammatically the chief of the features we have mentioned as characteristic of reproduction in fresh waters, namely, seasonal adaptation, large eggs

rich in yolk, slow embryonic development. But here there is also a long-lived larval stage : the tadpole of the leopard-frog lives for a year before its metamorphosis, that of the American bull-frog twice as long. By contrast with the insects, in Amphibia aquatic breeding has hereditary significance, and many Amphibia which, when adult, never enter the water, such as tree-frogs and salamanders, still maintain the habit, hanging the spawn on plants, to be washed into the water by rain, or placing it in burrows on the bank. Most newts do not completely desert the aquatic medium, but return to it to breed, and usually place the jelly-coated eggs under stones or plants in water, but some water-salamanders of America and Asia coil around the eggs to guard them, or wind them in strings about their own bodies.[35] But there are no such remarkable instances of parental care as in many terrestrial Amphibians, a fact which must be related to the more favourable conditions in water, and especially to the opportunity which this medium provides of protecting the eggs by simply enclosing them in gelatinous material which adheres to solid bodies automatically. We have seen how frequently this device is used by many unrelated animals which breed in inland waters.

An interesting fact in connection with the life-histories of Amphibia is the readaptation of certain of them, such as the giant salamander of Japan, to life completely in the water. A prelude to such a return may be the incidence of neoteny, or the attainment of sexual maturity during the larval phase, which thus obliterates the "adult" terrestrial phases. Neoteny is apparently the rule among the newts of some South Alpine lakes : in the famous Mexican axolotl (*Amblystoma tigrinum*) it occurs, or fails to occur, in accordance with the prevalence of moist or dry conditions, and in the *Amblystoma* of the Rocky Mountains it is not known at all.

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CHAPTER V

THE DISTRIBUTION AND DISPERSAL OF FRESHWATER ANIMALS: INFLUENCES OF THE GREAT ICE AGE IN EUROPE

> "What should we do but sing His praise
> That led us through the watery maze
> Unto an isle so long unknown
> And yet far kinder than our own."
>
> ANDREW MARVELL.

ON superficial consideration, the fauna of each inland water-system might well appear to be locked in its own more or less narrow confines and prohibited from spread or communication with that of neighbouring areas. Watersheds, mountain ranges, and even level land-tracts, must seem to constitute effective barriers to animals adapted for aquatic life, while, as we have seen, the saline waters of the ocean set a limit to downstream migration in all but a few highly exceptional cases. Notwithstanding the presence of these barriers, there is a certain sameness in the freshwater fauna of even widely separated areas which has earned for the life of inland waters in general a reputation for "cosmopolitanism" which is to some extent deserved. It is true that, as we have already suggested (Chapter I, p. 22), this general sameness of fresh-water types is partly a superficial character, due to the prevalence of species of small individual size and inconspicuous coloration; but there is still sufficient truth in the conception to render its further examination profitable.

The term "cosmopolitan," as applied to a biological species, must indicate that its members are to be found in all quarters of the globe, wherever the environmental conditions may be suitable for their establishment. Although at present we can lay no claim to full knowledge of the freshwater fauna

of our globe, still that of a great portion of the Northern Hemisphere and, in less detail, a few districts of Africa, Australasia, and South America, has been sufficiently well explored to enable us to establish with a good deal of certainty a cosmopolitan character (in this biological sense) for quite a number of freshwater species, representing a good variety of natural groups. Notable examples are *Arcella vulgaris* and *Ceratium hirundinella*, the common *Hydra*, *Cristatella mucedo*, and *Plumatella repens* (Polyzoa), *Chydorus sphæricus*, *Eurycercus lamellatus*, *Acroperus leucocephalus*, *Daphnia longispina*, and *Bosmina longirostris* (Cladocera), *Polyarthra platyptera*, *Notholca longispina*, and *Anuræa aculeata* (Rotifera), *Cypria ophthalmica* (Ostracoda), and *Limnæa pereger* and *L. stagnalis* (Gastropoda). As a concrete instance, the Copepod *Cyclops fimbriatus* has been found by naturalists in every country of Europe, in North and South America, in the Azores and other island-groups, in Ceylon and in Zanzibar, in water-bodies between sea-level and a height of nearly 3000 metres! Species of such extremely wide distribution are usually eurythermous and euryhaline (*i.e.* tolerant of a wide range of temperatures and of salinity), but forms less tolerant, and so restricted to water-bodies of some definite type, may still rank as cosmopolites in the true biological sense, as is the case with the brine-shrimp (*Artemia salina*) and the larva of a certain Dipteran (*Ephydra*), which occur in saline inland waters (but never in the sea) in regions so widely separated as the Western United States, North Germany, Transylvania, and the Aralo-Caspian basin.

But for the greater number of freshwater types no such cosmopolitan character can be established: extended investigations bring to light more and more distinct species in the several regions of the world, as well as sub-species or local varieties in ever-increasing number, while whole genera and even families of many groups are quite definitely limited to particular areas. The example of the Salmonidæ may be cited; all members of this tribe, which includes salmon, trout, sea-trout, and "whitefish," are confined (except for periodic sea-journeys on the part of migratory species) to

rivers of the Northern Hemisphere fringing the North Atlantic and Pacific Oceans, while the one species, *Salmo salar*, is entirely limited to rivers opening into the Baltic and North Atlantic: its nearest relative, the "Huchen" (*S. hucho*) of the Danube basin, is considered to be a sub-species of *S. salar*, derived in consequence of geographical isolation. The species of *Coregonus*, in the same family, are numerous and strictly limited in geographical range; in Switzerland and in our own country each separate lake basin has its own species or sub-species of this genus.[1, 2]

Mollusca as a whole, and the Lamellibranchia in particular, have very little cosmopolitan tendency: even within the bounds of Europe, the range of particular species of freshwater mussels (Unionidæ) is limited by watershed barriers between the river-systems,[3] though small types like *Pisidium* and *Sphærium* have a much wider range. The families of Neritinidæ and Ampullariadæ are confined to tropical and sub-tropical waters. Among Crustacea only a bare half-dozen Ostracod species are cosmopolitan in any sense, while species of the Centropagidæ (Copepoda) are so definitely regional in occurrence that they have been used, as will appear later, for zoo-geographical zonation; the genera of *Bœckella*, *Pseudobœckella*, and *Gigantella* are limited entirely to South America and the Antarctic islands[4]; Australia, again, has its own endemic Copepod genera. Among the larger Malacostraca the genus *Astacus* includes the common crayfishes of Europe and the Western United States; in Eastern North America its place is taken by *Cambarus*, which has only one European species (a cave-dweller); the Australasian genera are *Astacopsis* and *Engæus*, while *Paranephrops*, *Parastacus*, and *Astacoides* represent the tribe in New Zealand, South America, and Madagascar respectively.[5] There is no monotony of repetition here!

Still, it remains obvious that the boundaries between freshwater-bodies are for many species not inseparable; the rapid settlement by pond-dwelling types of artificially dammed fish-ponds, or of backwaters cut off from the main courses of rivers, may serve as illustrations of the ease with which such

barriers may be surmounted. Active migration from one pool or stream to its neighbour, especially over wet and marshy ground, is possible to many true aquatic types: the example of the eel, which can traverse considerable stretches of practically dry land, is certainly exceptional, but every naturalist knows that pond-snails, aquatic worms, and insect-larvæ of many species can survive long periods out of water, in moist air or weed, and many such undoubtedly do travel overland to some extent. The *transient* population of inland waters—those insect or amphibian types whose adults leave the water for a season—have special facilities for migration of this kind, and the dispersal of eggs by the winged imago is undoubtedly an explanation of the wide geographical range of many an insect species of this class. But even to these a mountain-range, or intervening sea, may prove a final barrier, and active migration on the whole is probably far less important in the dissemination of freshwater species than is their passive transport by external agencies. Among such, human agency has doubtless played some part. We have seen that the spread of *Cordylophora*, a brackish-water type, into the inland waters must be referred to human operations, and in many cases the transference of truly freshwater types takes place with far less physiological difficulty: even the energetic field-naturalist may be unconsciously responsible for extending the range of a species, as he empties the residue of his collections of the day into some convenient pond or stream. But far more constant than man's influence is that of animals which come habitually to the waterside to drink or feed, and carry with them mud or strands of weed, entangling small freshwater creatures, to their next resting-place. The most important of these visitors are birds, whose power of flight extends their active range so greatly, and little less considerable than their agency is that of winds. At first sight, dispersal by such means might seem to present little less difficulty than active migration, since any animal so carried must endure desiccation in transport: actually, many of our small freshwater forms are very easily transported in their ordinary condition by the agency of birds. A small *Pisidium* or *Planorbis*, lying already buried in the mud,

can be picked up within a clod of very slight dimensions on the foot of a wading bird, and has only to withdraw within its shell to secure itself from temporary danger; *Pisidium* and *Sphærium*, indeed, will often fix themselves directly to the toes of birds, newts, or frogs, gripping them between the valves, and may so be carried, while *Ancylus*, young pond-snails, and even caddis-larvæ must be frequently picked up in tangles of weed, and may sometimes be found upon the feathers of water-birds.[12] But in all cases of long-distance distribution by birds, and in all those in which wind is the agent of transport, the species which benefit are those which at some stage in their life-history form small, compact, and drought-resistant resting-bodies. How common is this practice among the freshwater fauna we have already seen; encystment of the whole animal against drought, and special production of spores, latent eggs, statoblasts, or winter buds, important as they are against the seasons' dangers, are certainly of no less consequence in this matter of passive distribution, and we should note their prevalence in just those types of animals whose bodily structure debars them from more active wandering, as Protozoa, Hydra, Rotifers, Polyzoa, and Entomostraca. Given such resting-bodies, often small and light, impervious to harmful influences, and capable of being drifted by currents, blown by winds, or carried by animal-visitors over dry land, the dispersal of members of the species and the extension of its geographical range become an easy matter. The range of such a species is thus extended not only in space, but in time also, since the continuity of freshwater life would else be gravely threatened by the impermanence of inland water-bodies: the great seas are permanent through ages, but change of form and evanescence are inherent in the very nature of the fresh waters. Even the largest lakes are slowly silted up and drained away by their incoming and outgoing streams, choked and overgrown by plant-invaders from the shore; the young torrential stream, constantly wearing down its banks and cutting through its bed, becomes in time a slowly-moving river, bounded by flats, and passing at last into a chain of swampy lakes which in their turn become dry land.

Even if we disregard the ultimate annihilation of every separate inland water-system, the continued evolution of their topography must involve grave changes in environment which would threaten the very existence of species once well established in them, were it not for those powers of resistance which enable so many of them not only to survive a temporary drought, but also to colonise new reaches against the time when the old become untenable.

A few examples of cases of endurance on the part of resting-bodies of various groups may serve to emphasise the amazing powers of survival which facilitate passive transport. The eggs of Rotifers retain their powers of development through many months of complete desiccation, and are often frozen for more than half the year in Polar lakes: temperatures of more than 100° F. below freezing-point, and even immersion for short periods in boiling-water, seem to do them no harm.[6] The statoblasts of Polyzoa develop better after desiccation and freezing than if conditions remain even: it may be that the splitting of their coats requires external aid.[7] Among Crustacea the eggs of Phyllopods have been known to survive and germinate after a period of desiccation lasting fourteen years,[8] and living Copepods have been obtained from clods of mud which had been dried ten years.[9] Perhaps the most surprising tale of all is that of the discovery of *Apus cancriformis*, in 1907, in a Scottish pool, after an absence of quite forty years from any British records[10]; it is not necessary to suppose that the latent eggs had been awaiting development all this time, but the probability that they were carried by some migratory bird from the Continent is no less striking an illustration of those powers of endurance which facilitate passive transportation. Another method of dispersal is suggested by some few records of successful germination of Cladoceran eggs taken from the stomachs of fishes[11, 12]; though transference by fishes could not extend beyond the bounds of the home-waters, yet the eggs may equally well pass unharmed through the food-canals of birds, and so secure a wider transit.

A zonary classification of the freshwater fauna as a whole

represents a more difficult undertaking than the establishment of such a series for either terrestrial or marine population, since we have here to deal with a greater constancy of type than in the former case, a greater variety of habitat than in the latter. Our consideration of one element in the freshwater fauna, the limnetic plankton of large lakes, is unhampered by any need to allow for marked discrepancies in habitat, and some serious attempts have been made to zone this fauna geographically. Even here, no hard-and-fast divisions can be made, as quite a number of the species in every area are cosmopolitans; all that can be done is to pick out peculiar types most characteristic of the separate areas, and for this purpose the most useful group is that of the Copepoda-Centropagidæ. Species of *Diaptomus*, in particular, are far more limited in range than those of *Cyclops* or Cladocerans; thus, North America has no fewer than thirty-nine endemic species of this genus, each with its own characteristic range, overlapped by those of other species [13]; in Europe certain *Diaptomus* species are confined to the far north, with Scandinavia, Greenland, and Iceland, others to the Mediterranean area, some to the eastern steppe-lands, and so on. Central, eastern, and tropical Asia, Australia, Africa south of the Sahara—all have distinct species of this genus, while South Amercia and such of the Antarctic islands as have yielded any records seem to have only their own peculiar Centropagidæ—*Gigantella*, *Bœckella*, etc.[14] Stingelin [15] has foreshadowed a zoning of lake-plankton based upon the distribution of Cladoceran genera, but in this group the species-limits, and even those of genera, are still the subject of much discussion, and in Europe, where most intensive studies have been made, and which at any rate concerns us most just now, such geographical zones as can be established are based on the distribution of *Diaptomus*. Steuer [4] elaborates from several sources a classification into four main zones, which are as follows:

1. A Northern, Arctic, and sub-Arctic Zone, including countries of the Arctic fringe and the great Scandinavian tableland.[16]

2. A North European zone, including the main plain of Europe north of the Alps and the German Mittelgebirge.
3. A Central European plateau-zone, from the Pyrenees through the Alps and Carpathians (including eastern and western sub-zones).
4. A Mediterranean zone.

While the last-named zone—the Mediterranean—includes a number of species peculiar to itself (e.g. *Diaptomus alluaudi*, *D. lilljeborgi*), which have local varieties in the smaller areas,[17] and both this and the eastern sub-zone have some forms in common with the eastward steppes (as *D. pecticornis*), over North-Western Europe generally we can distinguish a certain progressional series, from the north downwards. The northern area contains by far the greatest number of plankton species of many genera: some are peculiar to itself, as *D. laticeps*, *D. glacialis*, *Eurycercus glacialis*,[18] and among its most interesting types are a few which have undoubtedly close marine affinities, species of genera prevailing in the plankton of the northern seas, as *Limnocalanus macrurus*,[19] *Eurytemora lacustris*, *Heterocope appendiculata*.[20] Passing across the European plain, we trace a gradual thinning-out of northern species: some few are altogether lacking south of the Scandinavian Plateau (as *Diaptomus laticeps*, *Bosmina obtusirostris*, *Bythotrephes longimanus*), while many others (as *Heterocope* and *Eurytemora spp.*) show progressive diminution in numbers and in individual size, going from north to south, and finally die out entirely.[21] But in the Alpine and Carpathian regions many of the northern species reappear: *Bosmina* species, such Copepods as *Cyclops strenuus*, *Canthocamptus cuspidatus*, *Diaptomus laciniatus*, *D. graciloides*, with *Holopedium gibberum*, *Polyphemus pediculus*, and a whole host of such, cold-water loving types, common in the north and absent altogether from the plain, or of sporadic occurrence, mostly in isolated waters of high altitudes, here come into comparative prominence again, along with those eurythermous cosmopolitans (as *Cyclops serrulatus*, *Cy. fimbriatus*, *Chydorus sphæricus*, *Canthocamptus minutus* . . .) which are everywhere important.

These features of more or less discontinuous distribution, as well as the better individual and numerical development of the stenothermous species in the far north (where, also, they often produce their eggs in larger clutches), might perhaps be referred merely to the survival of such cold-loving types in any more or less favourable water-body, whose temperatures did not rise too high, which could be colonised in the course of chance passive distribution taking place as described above. Even so, we must suppose the stenothermous fauna to have some definite place of origin, some centre for distribution, and all arguments point clearly to a northern—perhaps Arctic—origin for many of these species. The theory of de Guerne and Richard (mentioned in Chapter I), so far as it applies to the limnetic plankton, receives strong support from the marine affinities of certain northern species; the facts of distribution, summarised above, seem to confirm it further; but perhaps more conclusive than either is the evidence derived from study of varieties and of life-cycles.

In all those planktonts which have alternations of sexual reproduction (leading to the formation of resting-eggs) with parthenogenesis, it has been considered—as already argued—that the former is the standard and more primitive method, the other but a later interpolation, though it may sometimes tend to swamp the original process. In Arctic regions,[22] and especially in Iceland,[23] Cladocera are always monocyclic, appearing early in the short summer from the newly-hatched winter-eggs, giving rise to perhaps only one or two parthenogenetic generations, and quickly forming individuals of the two sexes, by whose agency the resting-eggs are formed again. But in the southern habitats of these species the parthenogenetic period is extended, and may cover many generations; further, polycycly frequently occurs, with two or more sexual periods, the first of which exactly corresponds to the northern period, and bears no reference to external conditions prevailing in the southern habitat. Other sexual periods (one or more) ensue after a much longer interval of parthenogenesis, and the last one coincides very well with the approach of winter conditions. In the higher Alpine lakes such species

are more nearly like their northern relatives in the course of their generations, for here they never have more than two cycles, usually both short, and these may sometimes fuse into a single cycle, in lakes of very great altitudes, where the summer season is short. The case of *Polyphemus pediculus*, worked out by a number of investigators in different areas,[24-28] may be cited as a type; such a sequence is the rule in Daphnidæ, and in these latter forms the polycycly of the plains may lead, by very great extension of parthenogenetic periods, to the elimination of definitely sexual periods and the establishment of acycly. Only among the dwellers in the north do we find a type of reproductive-cycle which may be held as primitive, although it might alternatively be considered to be reduced in scope by the shortness of the summer season. Among the plankton Copepods and Rotifers the relations, though less elaborately investigated, seem to be very similar. The northern forms of many species reproduce only, so far as is known, by resting-eggs, while parthenogenesis and quick egg-development prevail towards the south; the condition is well authenticated especially in the case of *Cyclops strenuus* and of some species of *Diaptomus* and Rotifers.[29, 30]

Evidence derived from study of varieties is also in favour of a Nordic origin for many plankton-forms. In several cases where two allied types, a northern and a southern, are known, the latter may be proved to be more specialised in details of structure than the Nordic, which is thus to be regarded as the type-form of which it is a derivative. Ekman[31] has shown this to be the case with the so-called "*arctica* variety" of *Bosmina longirostris*; *Daphnia zschokkei* of the Alps is now held to be a derivative of *D. abbreviata*, a northern form; *Diaptomus bacillifer*, constant to type in northern areas, splits in the south into an Alpine variety and an eastern form peculiar to the Tatra[32]; and in the Alps *Bosmina coregoni* is now established as a derivative of *B. obtusirostris*, the standard Nordic form. There are, indeed, so many varieties and "local races" of *Bosmina* and the Daphnidæ, especially, within the southern area that endless attempts at re-classification of species and varieties have failed to determine

satisfactorily the limits of the several forms,[32] though in the north the species are far clearer and more constant to type. This variety building of the south is doubtless to be attributed to the increase in the number of parthenogenetic generations, giving increased scope for variation, while the relative frequency of sexual reproduction in the north tends to conserve the type, and may also counteract the effects of geographical isolation in the several lake-basins by ensuring formation of resting-eggs, for passive transport from one lake to another, though this factor may be insignificant, as we shall see.

If we accept the view that much of the European plankton is of Nordic origin, the manner of its passage southwards must yet be determined. Active migration is clearly impossible for plankton-types, and passive transport is in their case not so easily to be postulated as for littoral species, as, in the first place, resting-eggs of most pelagic forms sink to the bottom mud. Further, we have seen that many species may cease to form resting-eggs in the plains, and also, certain others may be absent altogether from these intervening regions, only occurring in the far north and again in the central mountain districts. The transport in such cases, and, indeed, in those of sporadic distribution over the plain, would involve tremendous journeys flown (if birds were the agents, and none others could have served) without a halt from the far north to some high Alpine or Carpathian lake. Only migrating birds perform such journeys, and, as Zschokke argues,[33] their spring northward flight occurs while the lakes are still frozen, so that by such agency we might expect a transference of fauna rather from north to south (as is the case) than south to north: but the conception is still difficult.

It may be that, in spite of difficulties, some transference of plankton species has occurred in this way; yet there are cases of species linking Nordic and Alpine fauna in which no theory of passive or of active distribution under such conditions as prevail in modern times can satisfy us, and for whose understanding another factor must be called in question. Study of a particular case will help to clear the issues. The best-established of all such examples is the distribution of a little

Triclad Turbellarian, *Planaria alpina*. This species, first found by Dana in the North Italian Alps, and named by him *Hirudo alpina*,[34] later placed in its true systematic position,[35] occurs in great numerical abundance in littoral waters of high Alpine lakes and in cold mountain-brooks of this and the Scandinavian area which are derived from the melting of glacier-ice and have a constant stenothermy, temperatures not usually rising above 11° C., even in summer.[36, 37] The worm, like other members of its tribe, is hermaphrodite, sexual maturity is rapidly attained, and reproduction takes place in

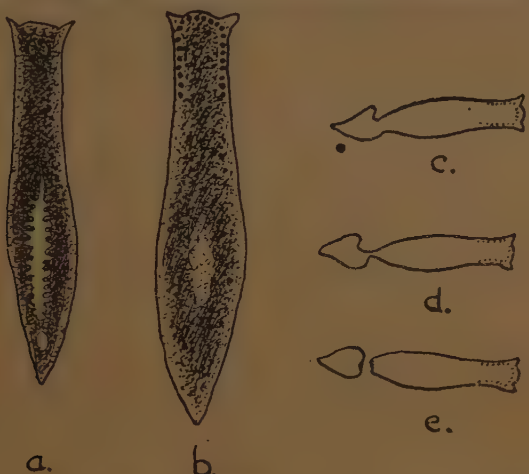

FIG. 52.—Two Turbellarian Relics of the Ice Age. *a*, *Planaria alpina*; *b*, *Polycelis cornuta*; *c*, *d*, *e*, three stages in transverse fission in *Pol. cornuta*.

Alpine lakes and streams throughout the year; the eggs are laid together in little spherical cocoons among the stones beneath which the animals shelter by day, emerging to feed at night. Between these two widely separated localities, the species has a peculiar and sporadic distribution right across the European plain; though never found here in lowland waters, it occurs in brooks in isolated patches of high ground, in the Harz and Eifel Mountains, in the Westphalian Sauerland, and so on, also on the Island of Rügen and in Britain.[38, 39, 40] Even within such areas it is found in little colonies, each one

isolated from its neighbours, occupying as a rule only the uppermost reaches of those brooks whose waters, drawn from deep springs, are stenothermous in a high degree. On the Continent it has never been found in water whose maximum summer temperature overpasses 15° C.; in one British area [40] the maximum is slightly higher, and *alpina* here occurs in some highland streams which are not fed by springs. In all these cases, the physiological stenothermy is very noticeable; a gradual rise of temperature in the laboratory through a few degrees beyond the normal for the habitat will kill the worm,[41] and other experimental evidence shows a marked preference for the lower temperatures and selection of an optimum of about 7° C.[40] In these scattered situations, sexual maturity is not perennial, as it is in the constantly cold waters of the Alpine Plateau, but it endures, with egg-production, throughout the winter months, and with the approach of higher temperatures the sexual organs degenerate, and a new phase sets in. "Buds" are cut off, by simple transverse fission, one at a time, from the hinder end of the body; each is, when first set free, devoid of eyes, head-organs in general, and pharynx, but within about ten days the young individual has the general anatomical features of the species. This process of asexual multiplication continues all through the summer months, until the water-temperature falls again to what has been called the "sexual-temperature"—about 7–11° C.[41] In winter, fission is very rarely seen, and never on the part of individuals with fully developed sex-organs, while the proportions of mature forms and individuals in fission during unstable seasons seem to bear a definite relation to the water-temperature—inverse for the former, direct for the latter.[40] The validity of this relation is further borne out by the observation that a sudden rise in temperature under experimental conditions may actually induce fission,[41] which, it has been suggested, is a semi-pathological phenomenon induced by temperatures higher than the optimum. Though this may be the case, it is a useful means of reproduction when sexual generation is denied, and the interpolation of the asexual phase is strikingly suggestive of analogy with parthenogenetic

extension in stenothermous planktonts in the lowlands. These modifications in physiology, as well as the distributional features, strongly suggest that *Planaria alpina* in the regions considered is not in its native habitat, but has made its way by penetration from its home in some far region of perpetual low temperatures, whether Alpine or northern, and in the highland brooks, with their comparatively stenothermous waters, founded cities of refuge. The question of its mode of

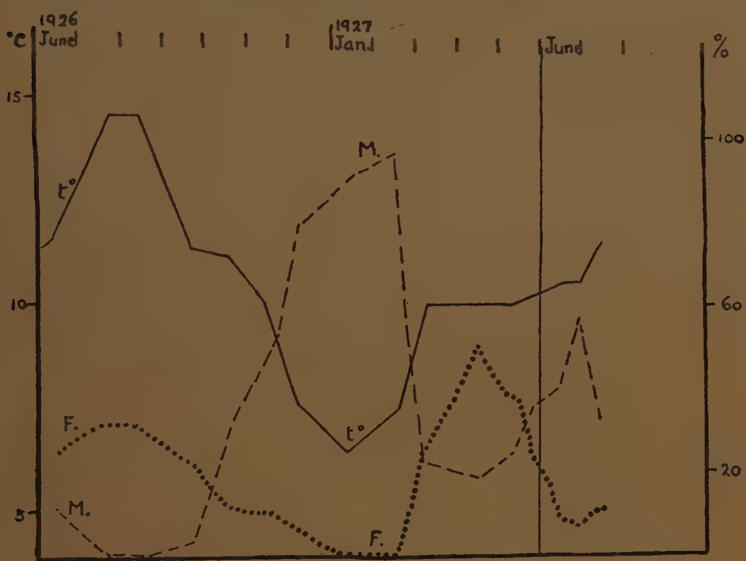

FIG. 53.—*Planaria alpina :* Sexual-maturity and transverse fission in relation to temperature of the water in Llanychaiarn spring (Carpenter). F, percentage of individuals in fission ; M, percentage of individuals sexually mature.

penetration is rendered difficult by the fact that neither the worms themselves nor their egg-cocoons can endure desiccation, nor is there any habit of encystment ; further, the cocoons are so placed in the brooks as to exclude the probability of transport by birds or other animals.[42] Active migration along stream-routes is precluded by the high summer-temperatures, and could not in any case account for the sporadic distribution ; it might take place to some extent in winter, when the lower

watercourses are cold, but, in fact, this species, unlike most current-dwellers, tends to move in the downstream direction when temperatures are even,[40] so that its penetration to the head-waters would still require explanation. The only supposition which can explain this widespread sporadic occurrence is that the species actively wandered into the lowland waters at some time when temperatures were consistently much lower than in our present age, and has since retreated to its stenothermous fastnesses, or been killed off from intervening reaches.

This assumption, which requires to be made in order to explain the distribution of many other species besides the one described as type, is amply justified by the overwhelming weight of geological evidence bearing upon the occurrence and extent of the great Quaternary Ice Age of Northern Europe and America. The ice-sheet of the Arctic Polar region, creeping steadily southward in the course of centuries, came to its maximum extent in Western Europe along a line passing through what is now the Thames Valley in Britain and across the continent roughly in the neighbourhood of 50° N. Latitude, ending some distance north of the Alps, which were then covered by an independent ice-sheet of lesser extent, touching the Bohemian Plateau and the Carpathians, and curving to the north again across Russia. As the ice-sheet crept lower, spreading before it cold and damp conditions, species accustomed to the low-temperature stenothermy of Arctic and sub-Arctic regions must have advanced before it, their home-centres being frozen, so no longer habitable, to find new homes upon that portion of the great European plain, between the northern and the southern ice-sheet, which still remained unglaciated. Here these Nordic types would mingle with a number of Alpine species, fleeing in similar fashion northward to a refuge on the plains from which all save the most resistant elements of their own fauna must have been gradually exterminated by the increasing rigours of the climate. It is true that this maximum extent of the ice-sheet, in which the free area of the plain was so greatly narrowed (probably to about 300 kilometres),[43] did not endure through-

out the two and a half million years at which the duration of the Ice Age has been estimated ; there were phases of advance and of retreat, but the last glacial period, being the one in which the maximum extent was reached, is all that need concern us as biologists, and during this there was sufficient time for profound changes to occur in the fauna of the European plain, ending in the establishment of a mixed fauna of very varied elements in the fresh waters. Besides the refugees from Nordic and from Alpine heights, all of them likely to be species accustomed to the prevalence of low temperatures, there must have been some remnants of the earlier fauna of the plain itself, either low-temperature stenotherms which had first had their homes in the coldest of its water-bodies or eurythermous types which would be easily adaptable, and doubtless in addition elements, similarly gifted with powers of endurance, derived from the fauna of the eastern steppe-lands by ordinary processes of penetration. Towards the close of the Ice Age, as the northern ice-sheet retreated gradually towards the Arctic Circle and the Alpine sheet also retired upon its centre, the steady rise of temperatures in the expanding intervening zone would overwhelm all but the eurythermous types, and stenotherms of Nordic or of Alpine origin would tend to follow the retreating ice northward and southward, so that in both zones, north and south of the warmer plain, the early fauna of post-glacial times would consist of species recruited from the glacial " mixed fauna " which had contained such diverse elements.

(These broad considerations must apply not only to the freshwater fauna, but also to land animals and to the flora, and in these latter cases parallel instances of distribution are not wanting. Indeed, the study of " Glacial Biology " was far earlier undertaken with reference to such, and is in some ways still further advanced than for freshwater types ; but the case of the latter, which is all that directly concerns us here, is perhaps particularly clear, in view of migration problems, and its elucidation has made great strides through the efforts of continental workers, led by the school of Zschokke.)

Active migration in the wake of the retreating ice-sheet

must have been a far easier matter for freshwater animals in early post-glacial times than such passage would be now, for then the melting fringes of the ice gave rise to great sheets of water, flooding the plain at first, and only gradually shrinking to the modern limitations of lake and river-systems. Early connections even across the present watersheds would be numerous and long-enduring, and the possibilities of active wandering, to a water-dweller, practically unlimited.

Not all the inhabitants of the inter-glacial plain would be thus driven to north or south: the eurythermous types which had survived the Ice Age would still find conditions tolerable, even in the warmer climate which ensued, upon the plain, and even low-temperature stenotherms could find a refuge here and there in special localities, such as springs, mountain lakes, and the deeper parts of lakes upon the plains, or subterranean waters—all of which, even to this day, retain a certain low-temperature stenothermy. The distribution of a species like our first example, *Planaria alpina*, is now clearly explained: living as a cold-demanding type upon the inter-glacial plain during the Ice Age, and driven from the larger watercourses, or killed off in these reaches, when the warmer climate thoroughly set in, it has survived in "relict-colonies" in the furthest fringes of these old haunts, in isolated patches of stenothermous water fed by mountain-springs. Even in such refuge-situations the summer temperatures rise beyond the limit of its old accustomed range, though not so high as to lead to extinction of the species, yet high enough to cause profound changes in its physiology, limiting the sexual period to the winter season (a reminiscence of the earlier climate), and leading to adoption of a new type of multiplication by simple fission in warmer months, when food is plentiful, growth rapid, yet the sexual function denied.

Less easy to determine is the exact place of origin of the species, its primal home before the Ice Age. We have seen that the mixed fauna of the inter-glacial plain included some very diverse elements, and out-going stenotherms might be derived from any one of several original sources. In such considerations, both geographical and physiological evidence

may be helpful; types of Nordic parentage would find the higher ridges of the Alps, which remained free from permanent ice throughout the epoch of maximum glaciation, and over which no waterways would lead continuously, an insurmountable barrier. We should not, therefore, expect to meet their representatives south of the Alpine heights, though the true Alpine forms, which were there before the Ice Age, might be found on both sides of the barrier, and incomers from the east would have their maximum development on the steppes. In the case of *Planaria alpina*, a Nordic origin is most probable, since apparently the Alpine barrier has not been overpassed: records of distribution are all from its hither side; but physiological evidence is held by some to be of a conflicting character. The species in the Swiss mountain-lakes, as we have seen, is sexual throughout the year, but in the Scandinavian area, so far as is yet known, the sexual reproduction does not occur in summer, even at low temperatures, which may be held as indication of its origin from Alpine stock; but records from the north are very few, and opinions differ as to the interpretation of the scanty facts.[44] Some types are clearly Nordic, as evidenced by distribution and physiology alike; among these, the plankton-species mentioned above (p. 113) are very conspicuous. The most rigidly stenothermous of the Nordic types, which were bound in close proximity to the fringe of the northern ice-sheet, never traversed the intervening plain to reach the Alps at all (as *Lepidurus arcticus*[45]). Some are to be found there only in small isolated colonies (*Bosmina obtusirostris*, *Bythotrephes longimanus*, *Diaptomus laticeps*[46]), and some few penetrated to the Carpathian fringe, which stood in close relation to the northern ice-sheet, but not across the plain to the Alps themselves: for instance, *Branchinecta paludosa*, which still survives in relict-colonies in the Tatra Mountains.[47] In converse fashion, some types of Alpine origin, especially many brook Hydrachnidæ,[48] have never spread northward across the plain, but are confined to these mountain-fringes. Finally, some Alpine types are believed to be endemic, of post-glacial development *in situ* from earlier wanderers since isolated in separate colonies

in cold situations, while others are incomers from the eastern steppes, where they now exist in greater numbers (*Diaptomus zachariasi*, *Asplanchna syrinx*[49]). Over all, the eurythermous cosmopolitans of indeterminate origin prevail.

The term "relict," as applied to a biological species, is capable of bearing many shades of meaning: it was first applied to species in fresh waters which, in view of some affinity with marine types, were supposed to have been carried into their present situations at times of over-flooding by the sea, and, while the waters of their habitat were gradually freshened by subsequent isolation, to have become slowly adapted to the new condition of reduced salinity.[50] On such grounds, all the pelagic fauna of inland lakes were once considered to be "marine relicts," and all the lakes containing plankton Crustacea, and Centropagidæ in particular, as "relict-lakes" derived from former arms of the sea. The discovery of the plankton-forms in volcanic crater-pools and in the lakes of high inland plateaux long since well isolated from the sea, reduced this theory to absurdity, as Credner demonstrated,[51] and the final standard of relict-status for a lake must be only the application of strict geological evidence. The newer use of the term "relict," to indicate a species, of whatever affinities, marine or inland, found nowadays existing in circumstances other than those in which it had its origin, is still capable of being diversely interpreted. By this broad definition (framed carefully, and with some difficulty, to exclude all question-begging), all species in the European area which have survived the Ice Age, except perhaps the eurythermous, rank as "relicts," whether their origin be local or remote; but some would limit the application of the term to such as can be proved to have their origin in other regions than those in which they now occur, and to have migrated, actively or passively, into their present habitats.[52-54] By such a standard, *Planaria alpina*, our type, must be a relict in the Harz and Eifel Mountains, and in those other isolated patches across the plain of Europe, but not a relict in those situations, whether Alpine or Nordic, whence it first started on its wanderings; *Polyphemus pediculus*, a relict in the Alpine zone

and on the plains, but not in northern lands—and so on. The difficulties of determining the exact place of origin are great for several species, so that perhaps a looser interpretation of the term is safer for our use; but even so, the relict status of each separate species can only be established after most careful consideration of the evidence of all kinds available, for its own individual case, and, unhappily, that fossil evidence which would be conclusive is not available for such fragile forms as are most of these freshwater types. Failing this, the criteria of Ice-Age relict status are most generally agreed to be as follows:

A. Geographical: the distribution centres in some particular area of low temperatures, where often the individuals are most numerous, robust, and fertile, and it is extended sporadically over a wider range, with special frequency in mountain regions.

B. Biological: the species shows a constant stenothermy, and most often the winter season is the active time; avoidance of strong sunlight is a frequent character (e.g. *Polyphemus*).

C. Evidence derived from study of life-histories: the sexual period is often limited to colder months; parthenogenesis or asexual multiplication may set in in summer time, with complication of the life-cycle (especially in Cladocera), and may lead to the formation of constant races, in cases of extreme reduction of the sexual phase (as in Daphnidæ), or of "summer-races," reverting to the type when autumn brings sexual union again (Daphnidæ and *Bosmina* of the Danish lakes,[54] also some Rotifers and *Ceratium*). In other cases, as in *Coregonus*, where sexual reproduction still prevails, the lack of means of passive or active distribution gives rise, by geographical isolation, to local races, varieties or subspecies in the newer habitat.

Another class of evidence is derived from study of the varying habitats dictated by the inherent biological stenothermy. *Planaria alpina*, as we have seen, outside the Alpine zone occurs exclusively in rapid brooks and springs, but within this zone it finds consistently low temperatures in the still waters of the plateau-lakes; many undoubted Ice-Age

relicts thus frequent the stenothermous waters of spring-brooks in the plain-region. Some types have a more complicated habitat-range: the water-mite, *Hygrobates albinus*, which lives in abundance in Norwegian brooks and in the cold low-lying ponds of Arctic Scandinavia, has in the lowlands found a cool retreat in the great depths of lakes, and *Lebertia rufipes* has a similar type of distribution.[55] Another deep-lake dweller, *Otomesostoma*, a Turbellarian, is littoral in high, cold Alpine lakes, and lives in shallow pools in the Riesengebirge.[56] The Ostracod *Limnicythere* lives in springs or in cold lake-depths alternatively, and many Cladocera which are littoral or pond-dwellers in the heights become pelagic in the warmer lowlands. Some species have found a refuge in underground waters, reached perhaps through springs: such will receive discussion in connection with the separate types of water-bodies, but we cannot leave the subject of the Ice-Age relict fauna in general without laying especial stress on the importance of springs, subterranean waters, and great depths of lakes, as well as certain cold, high moorland waters, no less than elevated plateau-lakes, for the survival of the stenothermous wanderers.

In some few cases of undoubted Ice-Age relicts a certain loss of physiological stenothermy seems to have taken place by adaptation: *Polyphemus*, though certainly a cold-water Arctic species, has been found existing in some scattered plain-localities as a more eurythermous type,[57] and certain other forms (Cytheridæ, *Plagiostoma* . . .) may have a very limited occurrence of this sort, while there is some evidence of adaptation on the part of *Planaria alpina* and *Polycelis cornuta*, another Turbellarian Ice-Age relict, to a slightly wider range of temperatures in Britain.[40] It may perhaps be the case that many of the true glacial relicts have lost their easily-recognisable character by adaptation of this kind. The distribution of one whole family, the Salmonid fishes, is particularly interesting in its relation to climatic changes during and after the Ice Age. The Salmonidæ are undoubtedly of northern origin: they are confined entirely to the seas and rivers of the cold and temperate zones of the northern hemi-

sphere, and are winter-breeders; the optimum temperatures for the development of the spawn are always low. In the brook-trout, the optimum lies between 1° and 4° C., and the maximum of toleration does not go beyond 15° C. It is certain that their range has been spread southward by migrations first induced by the extension of the great ice-sheet over the northern continents and seas, and the post-glacial shrinkage of the continental water-systems has cut off some members of the tribe belonging to the genus *Coregonus*, isolating them in lakes where many distinct species have become differentiated; in a similar way, *Salmo hucho* has been confined to the Danube reaches, being unable to journey

FIG. 54.—*Mysis relicta*, ♀ (enlarged about 4 times) (after Brauer).

downstream and encounter the warmth of the Black Sea waters. According to a continental theory, the race were denizens of the fresh waters before the Ice Age, and the migratory species acquired the habit of journeying to the sea in consequence of the scarcity of food in continental waters during the cold epoch; if this be so, it affords a fascinating parallel with the suggested origin of the wanderings of European migratory birds. But other authorities incline to the belief that the tribe is fundamentally marine in origin, and that the freshwater species are derived from "lag-behinds" of a stock whose breeding migrations were of the ordinary anadromous type exhibited by a number of other fishes, undoubtedly belonging to the seas [58] (see Chapter VII, p. 174).

Besides the glacial relicts of purely freshwater origin, we have to recognise another class, which may be called "marine"

with greater reason than underlay the early application of that term to plankton types in general. This class is represented chiefly by three small Crustacea, common in the lakes which fringe the inner Baltic, and in some Danish and Pomeranian waters.[59-63] *Mysis relicta*, a small Schizopod, so nearly like the marine species *M. oculata* that some authorities would class it as a mere variety, *Pontoporeia affinis*, again a member of a marine genus, and *Pallasiella quadrispinosa*, of similar affinities. To these must be added *Mesidothea* (*Idothea*) *entomon*, a large Isopod found only in Swedish lakes[60]; while *Mysis relicta* has a wider distribution than the rest, outside this special area, and occurs in Britain[64-66] and in Lake Superior and one or two other lakes of North America.[67] These types are usually to be found in the deep water, and appear to shun the open, sunny patches, especially in summer[59]; the reproductive season is typically winter, though it may extend further if temperatures remain low. In these respects they resemble typical Ice-Age relicts, but they have not penetrated southward across the plain, and all the evidence points to their origin from marine types at a late period, when the inland ice, already much restricted in extent, still covered Scandinavia, but left the Baltic regions, through the White Sea, flooded with icy water from the open ocean.[59, 60] This water-tract (known as the Yoldia Sea, from remains of the small marine mussel *Yoldia arctica* still found sub-fossil in the deep deposits in Baltic lakes) contained no doubt many marine species, but subsequent upheaval of the northern coast cut off its opening to the Arctic Ocean, and now the waters of the Yoldia Sea, freshened and swollen by the melting glaciers, became by slow degrees an inland lake of low salinity. During this gradual change, some of the more resistant marine types became adapted to the new conditions, while others of true freshwater origin came from the neighbouring areas to join

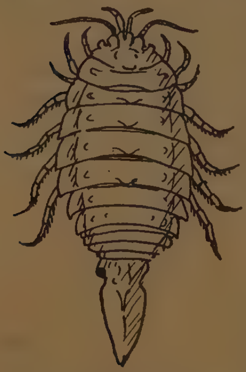

FIG. 55.—*Idothea entomon* (after Semper).

them: among the latter were a number of small Mollusca, such as *Limnæa ovata* and that other which has given to the area its name of "Ancylus Lake." Still further changes came: the climate softened and the western shore of this great lake subsided, possibly under the weight of melting ice, and through the gap the salty water of the North Sea streamed in, annihilating most of the new freshwater fauna and introducing once more marine types, this time derived from a western sea, among them *Litorina litorea*, from which the name of "Litorina Sea" has been derived. *Pallasiella*, *Mysis*, and the rest, now fully established as freshwater types, but destined apparently to a life of persecution on the part of the elements, retreated before this salty flood to the confines of the lake, and finally, the whole original body becoming saline, survived in scattered colonies only in isolated lakes cut off from the main mass by shrinkage (for the climate of the Litorina Age was a warm one), and so remaining fresh. An interesting feature which requires some further explanation than it has ever yet received is the presence of a *Mysis* of apparently the same species in the British and North American areas. In Britain, as well as being present in the Lake District, it is found in Lough Neagh in such quantities as to form a most important item in the diet of the pollan, a *Coregonus* species peculiar to the lake: indeed, its first appearance in the district was amongst the stomach-contents of that fish, as registered by Thompson,[68] long before its relict-status had been established by continental workers. Its habit of remaining near the bottom during daytime makes it difficult to catch (except for bottom-feeders), and it is possible that the species may occur, unknown, in a number of our British lakes; at present it is recorded also from Lough Corrib and Lough Erne—an interesting point, in view of some geological evidence that Lough Neagh once drained down into the latter lake.

Some fishes, also—a smelt (*Osmerus eperlanus*), a perch (*Lucioperca lucioperca*), and a bream (*Abramis farenus*)—and a Mollusc (*Neritina fluviatilis*) and a prawn (*Gammaracanthus loricatus*), found in Swedish and Finnish lakes, and some of them in Lake Furesö in Denmark,[61] are classed according to

their probable origin as "glacio-marine": these probably became adapted later than the others, during the freshening of the Ancylus Lake.

There still remains another class of relicts, once believed to be marine, whose origin requires discussion; but before passing to this separate topic it may be well to summarise the changes in the freshwater fauna of North-Western Europe due to the Ice Age.

First came, undoubtedly, extinction of many older types unable to endure the increasing cold: of these we have no record, but reason tells us that such a process did take place, as also that a number of eurythermous possible cosmopolites survived unmodified. Next, we must reckon with the mixing of the Nordic and High-Alpine types upon the cold and swampy tundra-belt remaining between the two ice-sheets. Retirement of the ice resulted in the gradual extension of a zone of warmer climate through Europe, and, at last, the shrinkage of the waters left behind, to settle into the modern river-systems and isolated lakes on plains and Alpine shoulders. During this period, some cold-loving species died out altogether from the intervening plain, their representatives remaining only in the far north and on the mountain-heights, while others, clustered in these separate areas, retained intermediate footholds only here and there in refuges provided by odd reaches of relatively stenothermous water. Some of these, now exposed to temperatures rather higher than their wont, have sacrificed the power of normal sexual reproduction for portions of the year, but learned to thrive on the more abundant food-supply of a warmer clime, and interposed a period of rapid multiplication, asexual or parthenogenetic, during the summer. The speedy course of such generations, or in some cases the in-breeding due to isolation in the narrow valleys, resulted in formation of some new varieties, sub-species, or even species, of Nordic types thus stranded in the plains. Last, the invasion of the Baltic area by flooding water from the Arctic Sea brought in a number of purely marine types, some of which have survived and been adapted, during the freshening of their water-body, into freshwater

species, which found a refuge in the lakes cut off by shrinkage when the invasion of the Ancylus Lake by the North Sea restored saline conditions.

The ice-sheet, spreading death and desolation before it in its progress southward, yet, in its retreat, induced an extension in the range of species, an adaptation in physiology and habit, and a formation of new local types, which must induce us to regard it as, on the whole, a progressive rather than a retrogressive force.

Our third and last-remaining class of relicts are to be found in certain large and isolated lakes, particularly Baikal, in Siberia, and Tanganyika, in tropical Africa, two of the largest bodies of fresh water in the world, both of which were thought for many years to contain a fauna of close marine affinities which must have been derived by gradual isolation from the sea. In neither case has exploration been so thorough as would be made of lakes more easily accessible, but special studies and collections have furnished evidence which in both cases may safely be accepted.

The case of Tanganyika is perhaps the less complex, though it has required a series of expeditions since 1858 to furnish what is still imperfect knowledge of the fauna and its relationships. The early finding of a Medusoid type, *Limnocnida tanganyikæ*, unknown at that time (1883) from any other locality, strengthened opinions previously formed, on grounds of the peculiar characters of certain of the Gastropod Molluscs,[69] which seemed strongly suggestive of marine affinities, that this lake was connected with the ocean in no far-distant geological time. The theory postulated a great extension of the Atlantic over the Congo Basin, to include all of the group of tropical African lakes, Nyasa, the Nyanzas, as well as Tanganyika; but geological evidence is firm upon the long-standing isolation of this area, and further finds of *Limnocnida* and its near relatives in several other freshwater

FIG. 56.—*Limnocnida tanganyikæ* (after Gunther).

localities (African, Indian, and Chinese) discredited its presence as a witness of marine influence.[70] Moore's expedition of 1895[69] paid special attention to Mollusca, and it was decided that the peculiar Gastropods, many of them endemic to Lake Tanganyika, and some to neighbouring lakes, had no close relation to modern marine types, but rather to certain Jurassic forms. The date of the supposed connection with the sea was now moved back into that period —but still the geological facts could not support it. Several more recent expeditions have made much larger animal and plant collections which have been carefully examined and reported on by specialists, and the general result is the recording of a peculiar "isolation-fauna" of endemic genera and species in almost every group of animals. Some species are endemic in each of the lakes: in Tanganyika are nearly 300, 121 of them fishes, with 55 endemic genera in this group alone—but every lake has some, the smallest least. The vexed question of the Molluscan types resolves itself into consideration of the Gastropods, since in Lamellibranchs the genera are such as *Unio*, *Corbicula* . . . clearly of freshwater stock. The Gastropods are certainly "thalassoid," or pseudo-marine, in appearance, especially in one family (Tiaridæ) which have heavy sculpturing and tubercles like those of marine types. But no close relatives can be found for them among modern sea-living forms, and the interesting suggestion has been made[71] that this may be a case of "convergence," and that the thick and sculptured shells are due to the salinity of the waters, induced by high evaporation; certainly considerable

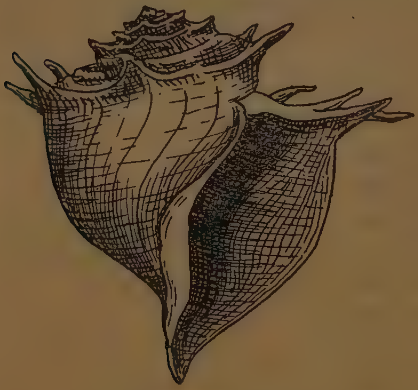

FIG. 57.—*Tiphlobia horei.* A fresh-water Gastropod of pseudo-marine type from Lake Tanganyika (after Hesse).

quantities of magnesium salts are present in solution. The Crustacean types are clearly of freshwater affinities: even the Brachyuran crabs belong to the Telphusidæ, a family of tropical freshwater forms.[72] Cladocera of the plankton of all these lakes (except of Tanganyika, which, curiously, seems to have none at all) are generally common cosmopolites, such as *Chydorus sphæricus*. The Rotifers are also cosmopolitan; but other groups whose distribution is of the active, not the passive type, have a rich development of endemic forms. By all the evidence the fauna is (excepting cosmopolitan intruders) an "isolation-fauna," specialised in a restricted area and under peculiar conditions from a freshwater population of great antiquity.

The fauna of Lake Baikal, like this other, contains endemic types in high proportion, especially among Mollusca, worms, larger Crustacea, and fishes. Species long thought to be "marine"[73] include a seal, a sponge (*Lubomirskia baikalensis*), and several fishes, but the sponge is now believed to be merely archaic, and the origin of the fishes debatable,[74] while in any case both these and the seal could be accounted for by trespass of the overflow of the post-glacial Ice Sea. Some species of worms and Isopods have most affinity with forms found in Oriental and American fresh waters[75]; a few cosmopolites occur, of course, especially among the planktonts, but the endemic fauna is peculiarly interesting. Giant Amphipoda of archaic type, related to freshwater Gammarids, are plentiful: among them, *Brachyurops grewingki* attains a length of nearly 10c entimetres, a phenomenal size for a member of this group. Some peculiar Isopods also occur, but in particular the fishes and Oligochæta have a high percentage of endemic types which, like some of the Mollusca living there, are clearly scions of an ancient stock of true freshwater types, long since extinct. The lake has been described in vivid phrase as "a zoö-palæontological museum"; there is no doubt that here, and in Tanganyika, the preservation of archaic types has been made possible by the long isolation of these lakes. Their age, their immense size and depth, contrasted with the shallow impermanency of most freshwater bodies, have enabled a

course of evolution to take place within them by which these antique types have taken on some of the superficial characters known elsewhere only in the open waters of the great seas. These lakes are of the highest interest, both as reminders of an earlier world and as examples of the progressive force of isolation.

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CHAPTER VI

THE BIOLOGY OF RUNNING WATERS: HEAD-STREAMS AND HIGHLAND BROOKS

"I'll tell you, scholar: several countries have several kinds of cadises, that indeed differ as much as dogs do . . . these be usually bred in the little rills, or ditches, that run into larger rivers."—IZAAK WALTON.

IN the foregoing chapters we have considered the life of inland waters as a whole, directing attention to its adjustment to those environmental factors which operate in the large in all such situations. It is now time to turn attention to the special features of each separate type of water-body and determine how far these features influence the life which characterises it.

Classification from this point of view is not an easy task. An obvious distinction may be made between the running waters and such still bodies as lakes and ponds, and we may designate the living organisms of the former as "lotic" (*i.e.* "washed"), those of the latter as "lenitic" (peaceful) in type, in the main; but we shall find that even so broad a generalisation will not invariably hold good. A river should be peopled by lotic types *par excellence*, but actually no river flows at an even gradient, or in a straight line from source to mouth, and every stream exhibits local variations in the speed of current ranging from the swift reaches down to the quiet pools and backwaters in which communities of lenitic type, practically indistinguishable from those of ponds, predominate. If such a difficulty confronts us in the establishment of our first grade of ecological classification, we must be prepared to find still greater anomalies as we descend to detailed study; it is, in fact, impossible to fix a rigid scheme of any kind for guidance in freshwater studies: any scheme adopted must be

as fluid as the medium which embraces the associations, communities, habit-groups—whatever we may choose to call them.*

With this preliminary caution, we may proceed to an outline-study of the life of running waters.

Nearly all rivers rise in high ground, drawing their supplies from such reserves of water—originally precipitated from the atmosphere—as springs, lakes, marshes, snowfields, and glaciers; their upper courses are typically swift, the gradient being steep, and stream-erosion very pronounced. In districts of hard rock (such are most highlands), the river-bed in this part of the course is therefore stony, cut down to "country-rock," and strewn with loose, torn-off blocks around which the current swirls, sweeping away pebbles and carrying in suspension all finer particles. (The diameter of solids which can be thus carried varies according to the velocity of the current: at 3 feet per second, heavy shingle can be moved from place to place; at about 5 inches per second, nothing larger than fine particles of clay.[1]) The course of such a stream is frequently erratic, as the water-level and force vary according to the seasons and secular changes in weather. In such a watercourse the keynote of the physical environment is restlessness: the rapid current makes establishment of plant-life difficult, by sweeping down all the loose particles from between the stones, so that only such plants as tufted mosses and encrusting growth of various kinds can get a hold upon the rock and boulders, and every mobile animal must guard itself against the peril of losing foothold and so being swept into another milieu. To balance these most trying conditions there are present certain factors advantageous for the maintenance of life, chief of which is the excellent aëration of the rapid, splashing water; another is its purity; a third, the constancy of its temperature, since it has not been long exposed to influences which might alter the character it derives from the conservatism of its sources.

* For a discussion of nomenclature, see 7, 15, 11, in this chapter's list of references. The writer is of opinion that nothing is to be gained by an attempt to define strictly terms intended to describe conditions and situations which are inextricably mixed in Nature.

As we pass down the stream we find the gradient usually lessens, the current becomes less rapid, and the bed deepens and widens, while the forces of land-erosion wear down the sides of the valley into an open V. The slackened current can no longer break off masses of rock and grind them into pebbles, but begins to deposit these pebbles, later gravel, and, later still, fine sand, upon its bed; rooted vegetation begins to get a hold, and by the binding action of its fibres leads to still further accumulations about the roots; the water-level is less variable, for floods and droughts are feebler in their effects upon the increased body of the stream. Oxygenation is less complete, the depth of water being greater and the motion slower; and the temperature, especially of the surface-waters, changes in closer accordance with that of the air, owing to the longer exposure to its influence and to the widening of the valley. Still lower in its course the river winds over a level floor of silt-deposit, forms meanders and loops in its course, and may even cut off backwaters which become stagnant; finally, it passes through a brackish estuarine zone to the sea.

Each portion of the river has its typical development of plant and animal life; these have been studied for the most part in isolated patches, and only two great continental streams, the Rhine and the Volga, have been surveyed with anything approaching completeness from the biological standpoint,[2, 3] but from collation of separate data a fairly complete picture can be drawn, and it is best to classify the courses of rivers under two main heads—the Highland Brooks and the Lower Courses; but we must remember in so doing that these two grade insensibly into one another in any actual stream, and, on the other hand, each one includes a number of sub-sections still less distinctly marked off.

A. Biology of Highland Brooks

A1. The Head-Streams.—In regions of steep gradients young brooks and rivers have great powers of erosion, owing to their rapid flow; but if we follow backwards along the course

of such a brook we find that it is formed by union of a number of much smaller streams, each leading from a water-reservoir (spring, marsh, or glacier) by an irregular course, often, because of the small volume of water, far less constant and well-marked than is that of the brook to make which it combines with several of its fellows. Such *Head-Streams* are the first of our series of ecological river-types to claim consideration. Features which have the strongest influence upon their population are the small volume of the water, its constant temperature, and the intimate relations which exist between water and land: for here the stream very frequently divides to form little branches which unite again, enclosing areas of wet earth or patches of stones washed on their undersides only, or covered by a thin layer of water.

In regions of great altitude, the head-streams which draw from glaciers are extremely variable in respect of volume; the melting of the ice in spring and summer may swell them into rushing torrents, turbid with earth and gravel, but in winter their water-content is very much reduced, and even they themselves may partly freeze. The water-temperatures of glacier-brooks in the High Alps, according to Steinmann,[4] reach a maximum of only about 3° C. in full summer conditions. This factor combines with their inconstancy of level and the instability of their gravel-strewn beds to render them entirely barren of established life, though a few eggs of insects may be deposited and hatch in them.

At somewhat lower levels, in head-streams which draw from mountain slopes or subterranean springs, the temperatures are higher. At about 2000 metres, in the Alps, they vary at most from 4° to 12° C. within the year, and many of them have a range of only 4° to 7° C.[5] In Poland, near Lake Wigry, Demel found a range of very slight variation about an average of 7° C. in head-streams drawing from springs at the base of a moraine.[6] Descending to regions well below the snow-line, we find the temperatures of spring-waters even more variable: in the lower Alps, Schwarzwald and Jura Mountains, Steinmann found an annual range of 5° to 7° C.; springs of the German Sauerland, at heights of 250–550 metres,

vary in temperature from 3·75° to a 14·75° C. summer maximum [7]; in the vicinity of Basel, the range is 2·3°–18·6° C., and in a hilly area in Wales, springs at an altitude of round about 100 feet were found to vary between 2·5° and 16° C. within twelve months of observation.[8] The range may seem a wide one, as compared with that in glacier-brooks, but actually these waters may be classed as "stenothermous," compared with those of reaches whose altitude may be no less, but whose open valleys and greater distance from the springs induce a closer approximation on the part of water-temperatures to atmospheric readings. Thus, in Steinmann's area, the temperatures of the brooks themselves covered a range of 5·5° to 13° C.; in the Sauerland the range was 0° to 20° C., and in the Welsh area temperatures of 2° to 22° C. were recorded for neighbouring brooks.

A separate discussion of the biology of the actual water-sources must be deferred, for reasons which will later be apparent (see Chapter IX); they have certain features in common with the head-waters which issue from them, and our summary of the life of these will be in part appropriate to the springs also.

At first sight we might be inclined to stigmatise the head-streams as biologically barren: only here and there a few close tufts of moss, encrusting liverworts, or slimy-coated Diatoms, grow close against the stones. No animals are visible, and we argue with justice that food is very scanty here, while the shallow water, continually streaming, independently acts as deterrent to the development of plankton and of nekton, and the absence of such fine bottom-detritus as collects about the roots of plants in quiet reaches discourages the settlement of a rich benthic fauna. But life is indomitably insurgent: no opportunity for its maintenance is ever neglected, and even in these unpromising situations we find each small advantage utilised to the full by living creatures. Lift a stone from the water's edge, and you will see some little animal scud hastily across to find a new retreat; carefully pluck a handful of the moss and shake it under water, and a whole company of small animals reveal themselves. These

are the tenements of the brook-fauna, in which the population—poor, it is true, but richer far than might have been imagined—ekes out a scanty living on a basis of nutriment provided by such plants as do exist. By far the greater number of citizens of this state are microphages, and strain the water for small particles detached from plants in process of decay and borne along the stream; others, small snails especially, rasp against the stones for Diatoms and other minute Algæ; and smaller still in numbers, though conspicuous because more active and of larger size, are the carnivorous aristocracy which capitalise this incessant labour.

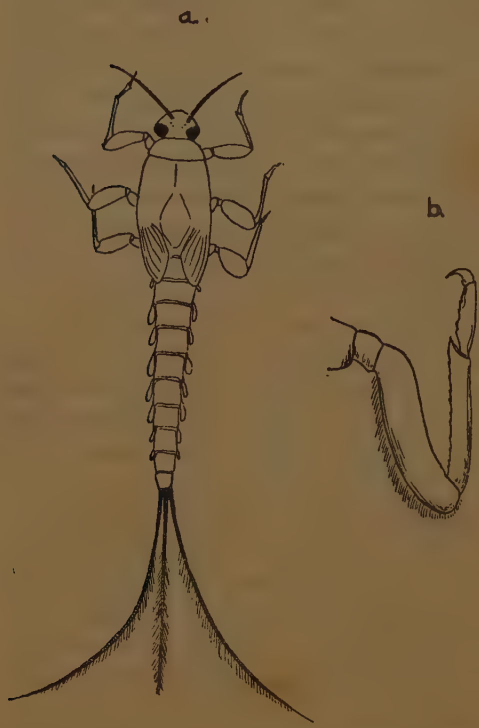

FIG. 58.—*a*, Nymph of *Baëtis vernus*, from a Welsh mountain stream, enlarged about 2½ times; *b*, first leg, on a larger scale, to show the strong hooked claw.

The fauna of the tufted Bryophytes includes a variety of microphages: Rhizopod Protozoa, like *Difflugia*, and Rotifers and little "water-bears," are common in it, and sometimes Copepods, especially *Canthocamptus*, which can crawl with wriggling motions of its worm-like body among the tufts. Even the larger Crustacean scavengers, *Asellus* and *Gammarus*, may shelter here, and little caddis-worms with light cases of mud and silk (as *Adicella*), or with leaf-fragments mixed (as *Crunœcia irrorata*) are very common, with some larvæ of

smaller Ephemerids and Plecoptera. One mayfly larvæ very often found in the moss-tufts is *Baëtis*, which scrambles actively about them, hitching on by its curved claws; *Leuctra*, *Nemura*, and *Isopteryx* are the most frequent of the stonefly nymphs. All these are microphages, as are the small Hydrophilid and Parnid beetles—especially species of *Elmis* and *Anacæna*—found in the moss in rather smaller numbers; quite a different mode of living is adopted by the little blood-sucking water-mites which cling by hooked claws to the moss, waiting their chance to fix themselves upon the bodies of its more peaceful tenants.

Among the pebbles, and crawling over them, a few small snails scrape off the Algæ with their horny radulæ. *Limnæa truncatula* is quite common here, and other species of *Limnæa*,

FIG. 59.—Cases of caddis larvæ from stony brooks. A, *Goëra pilosa*; B, *Silo nigricornis*; C, *Apatania fimbriata*; D, *Stenophylax nigricornis*; E, *Agapetus fuscipes*. (All slightly enlarged.)

as well as *Bythinella*, may occur. Beneath the stones, and in their crevices, some larger caddises than those of the moss are to be found; delicate types with weak, soft cases would be in danger here, in the grinding of the pebbles, and those which flourish are especially *Agapetus*, *Stenophylax*, and *Apatania*, which make firm, well-built cases of small pebbles. Most common of all stone-sheltering animals here are small Planarians, whose flattened bodies cling so closely to the stones, and fit themselves so well into their crevices, that they escape destruction, though so soft and delicate. *Planaria alpina*, which we have already recognised as an Ice-Age relict, finds in these reaches, with their low-stenothermy, a convenient refuge: as we have seen, it is common in Highland spring-brooks over most of Europe. *Polycelis cornuta*, like

alpina, a dark pigmented form with prominent head-tentacles, but bearing many marginal eyes in place of the two which characterise *Planaria* species (see Fig. 52, p. 115), is also common in head-streams, but, though stenothermous, and judged a glacial relict, it can endure a wider range of temperatures, and is often found in reaches just below this topmost zone. Its penetration of European waters most probably took place towards the close of the Ice Age, when water-temperatures were slightly higher and more variable than just previously, in the palmy days of *Pl. alpina*.[7] Both species prey on insect larvæ, and on Amphipods and worms, when they are to be found, but Steinmann believes they eat decaying plant-material if other nourishment runs low. Some eurythermous Triclads, such as *Polycelis nigra*[4] and *Pl. albissima*[8] are sometimes found in the more muddy of the head-waters, and in these the scanty benthic fauna is further supplemented by the accession of small bivalves of the genus *Pisidium*, which includes the most diminutive species of the group, and little Cyprids may be numerous in similar situations.

Besides moss-dwellers and stone-shelterers, the fauna of these reaches includes a class of very special interest: small, fragile creatures which can find a lodging in that thin film of water which surrounds the surfaces of stones not truly submerged, and clings to them by surface-tension; these constitute the "*fauna hygropetrica*."[7] The most familiar of its species, and the easiest to recognise, is the larva of the midge *Dixa maculata*. It has a worm-like body, which it keeps bent in a U-shape, and wriggles against the stone, pushing with head and tail, so that the bend of the U is thrust forward in its clumsy, but rapid progress. Like so many larvæ of Diptera, the *Dixa* breathes in atmospheric air, thrusting the hinder end of its body, which bears the open spiracles, through the surface-film. Other Dipteran larvæ which adopt this curious mode of living in the thin water-layer, either on stones or on the fronds of mosses, or even drifted leaves, are *Orphnephila testacea* and *Pericoma canescens*, while *Tinodes* and *Stactobia*, among the caddises, are also members of the film-fauna.

PLATE
III

IIIa

IIIb

(*a*) Near the source of a Welsh highland brook. The stony beach in the foreground shelters a lithophilous fauna poor in species and including the Ice Age relict, *Planaria alpina*.

(*b*) The trout-beck below the cascade-reach. The stream is still swift, and lithophilous types predominate, but *Planaria albina* is replaced by *Polycelis cornuta*, and a number of moss-sheltering types accede.

To face p. 142.]

Consideration of these types leads on to mention of an ecological association of another type—or types—found near the margin of the water in wet earth or gravel or in damp

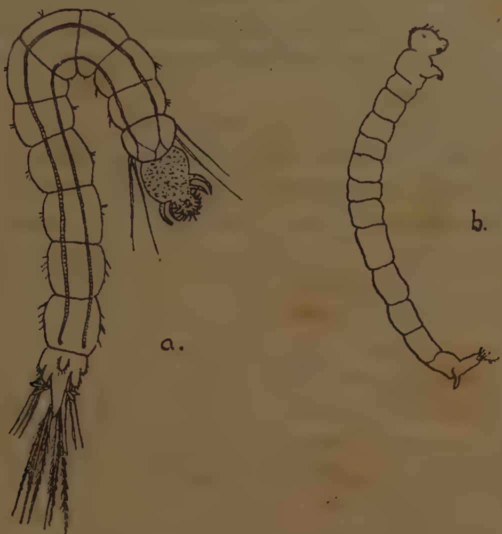

FIG. 60.—Two hygropetrical Dipteran larvæ. *a*, A *Dixa* species; *b*, *Orphnephila testacea* (after Thienemann).

patches under stones, a set of very mixed affinities. A number of larvæ of Diptera, characteristic of wet earth in general, not limited to the true water-bodies, may be found here, including "leather-jackets," the larvæ of crane-flies (Tipulidæ). The

FIG. 61.—Larva of *Pedicia rivosa* (after Oldham).

great carnivorous larva of *Pedicia rivosa* (Limnobiidæ) may perhaps be called a genuine aquatic, but often in its close proximity we find a number of truly terrestrial animals: spiders, Phalangids, Staphylinid beetles (especially *Dianoüs* and *Lesteva*), which for some reason seem to find these damp localities congenial. Lifting a stone just at the water's edge

one sometimes sees a little cluster of these land-animals beneath it, as well as spring-tails, which so often hop upon the surface-film of quiet waters. Whatever be the attraction that draws them hither, it is certainly not the presence of a rich food-supply; probably a combination of light-shunning and avoidance of dry air with its rapid changes of temperature explains their presence.

Besides the ecological considerations, another aspect of the life of the head-waters is of the greatest interest, and deserves closer consideration than we have yet afforded it. The stenothermy of these waters makes of them a splendid refuge for all species sensitive to heat, especially the Ice-Age relicts: Among these we have already noted the two Planarian species, but almost every group of animals here represented has its relict-species. The Rhizopoda of the moss-tufts most often belong to species found also in cold depths of lakes and other refuges of such relicts. *Difflugia pyriformis var. lacustris*, *Nebela vitræa*, and others, common here, were first described as Ice-Age refugees sheltering in the depths of Lake Leman [9]; a *Cyclops* of the moss (*C. strenuus*) has all those features of distribution in other sites, joined to a very constant stenothermy, which characterise the relict-species (see Chapter V). Many of our Hydrachnidæ are known for relicts; of these, *Hygrobates norvegicus* and several species of *Feltria* and *Lebertia* [10] are of frequent occurrence in head-waters. A number of Trichopteran species, common in Alpine and in Nordic areas, such as *Stenophylax picticornis*, are also classed as relicts. The species named is interesting in exhibiting some adaptation to a change of climate, in the shifting of its reproductive season from summer back to early spring, a change which seems to indicate survival from colder conditions.[4]

To summarise: factors which influence the development of the life of the head-streams are (*a*) shallowness and inconstancy of course, (*b*) a low range of temperature-variations, (*c*) scanty food-supply, conditioned by purity of the water and infrequency of vegetation. The biocœnosium of these streams includes (1) in numerical supremacy, microphagous types which shelter in the moss or among sediments, or lead

a hygropetrical existence in the thin water-film on leaves or stones, (2) a few direct plant-eaters, mostly snails, (3) carnivorous Planarians and blood-sucking Hydrachnidæ; the latter lurk in moss, the former under stones.

A special feature of the fauna is the frequency of stenothermous relicts of the Ice Age, which generally outnumber the few eurythermous types.

A2. The Trout-Beck.—Sooner or later, the head-streams unite to form watercourses of more constant flow and greater volume, with sufficient force to wear their rocky floors into definite channels which remain permanent, although in flood their boundaries may be exceeded. The current here is usually much more rapid than near the source, partly from the greater volume of the water, partly from the erosion of the channel into a sharper gradient, cutting backward, and, while the stenothermy of the head-waters is pretty well maintained by the rapidity of flow, other conditions alter. In particular, the water deepens, and its power of carrying objects in suspension is greatly increased by the gain in speed, so that the finer grades of sediment which sometimes lie along the course above can find no lodgment here. In a typical highland brook, the rocky bed is strewn towards its sides with rough boulders and coarse pebbles, and only at angles in its course, where the flow is slackened around some obstacle, rough grit may be deposited.

The dominant features of this environment, considered as a home for living beings, are stenothermy, strong current-force, changes in water-level, oxygen-saturation of the water, hard rocky bottom, and consequent scarcity of plant-growth: this last, indeed, is even more poor than in head-waters and consists of the same few elements. By contrast with the upper region, in this the dominant factor in the lives of stream-dwellers is the great force of the rushing current, rather than shallowness of the water, which played so great a part in the higher reaches. In spite of increasing volume, the water here is too swift to allow plankton to develop, and the few nekton-types which may occur are either powerful swimmers like the trout (*Salmo fario*), which gives its name to these, its favourite

reaches, or, like the miller's thumb (*Cottus gobio*) and loaches (*Cobitis* and *Nemachilus*), spend most of their time sheltering among the stones. The dorso-ventral flattening of the body in *Cottus gobio* is a nice adaptation to the sheltering habit; this little fish is far more common than is generally supposed, but usually eludes observation: if its stone be moved, it darts away to another too swiftly for the eye to follow it. All weaker members of the nekton are eliminated; we see here no swimming beetles or Hemiptera, and all brook-mites—

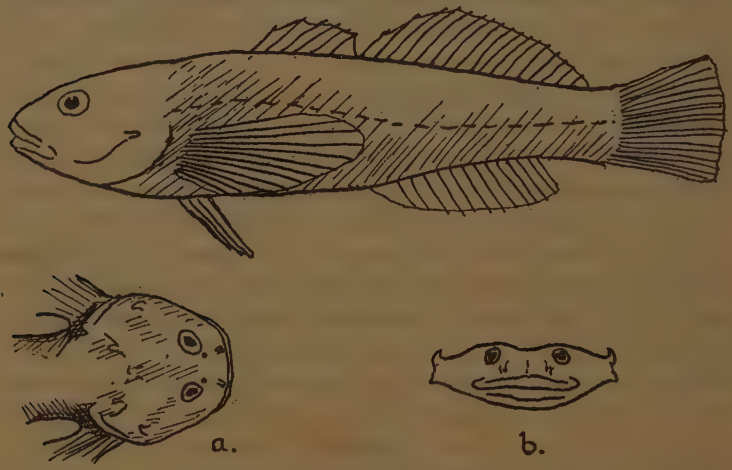

FIG. 62.—The Bullhead, or Miller's Thumb (*Cottus gobio*). *a*, Dorsal view of head; *b*, head seen from front.

whose cousins in still waters have long legs fringed with hairs to act as paddles—have short, stout limbs with claws curved into hooks for scrambling.

The force and constant swirling of the water renders existence quite intolerable for animals needing to take air at the surface, and so we notice a deficiency of larvæ—especially those of Diptera—with open spiracles. How to endure the current is the problem of greatest urgency for the brook-fauna, and in the many devices used to solve it we find especially a cunning use of one of its own important consequences, the presence of rough stones along the bed. The burrowing

molluscan and worm-like types which may occur in head-streams can find no footing, but the lithophilous fauna, of animals which use the stones as shelter, reaches here its full development, and includes a very great variety of species. The vast majority are to be found *under* the stones, and among these certain mayfly and stonefly larvæ are especially conspicuous, by reason of their size. The general type of form in these is closely related to the clinging habit; in contrast to the species which live in sand or vegetation, they present a broadening of head and body, by lateral expansion, and there is strong dorso-ventral flattening. The legs are long, and are set at the sides of the thorax, with coxæ widely separated, and all the joints are often flattened in the general plane. In clinging, the six legs are radially out-spread like limbs of a grapnel, holding by the claws to small irregularities of surface, and the flat head and body are very closely pressed against the stone. The gait is a sideways scuttle, strongly reminiscent of that of a crab. The analogy is justified, since flattening and radial spreading of the limbs serve the same purpose here as in the wave-washed zone—to give a firmer hold. Any one who has tried to collect larvæ of *Ecdyurus* or of *Dictyopteryx* has had good opportunity to realise how this flattening serves them. Disturbed by the light, they move around the stone so closely pressed to it that they seem to be part of its own substance, and they can only be removed with patience—and a brush. Steinmann has drawn attention to the value of this flattening, not only as presenting a broad adhesive surface, but also in minimising surface-resistance to the current, and in this latter connection there is also value in the marked reduction of the fringing hairs on body-segments, limbs, and caudal styles which we notice in these current-species, when

FIG. 63.—Fourth legs of Water-mites of two species of *Libertia*. *a*, *L. complexa*, found in the mossy tufts of swift brooks; *b*, *L. insignis*, a swimmer, found in ponds (after Thienemann, from Viets).

we compare them with species of different habit. Perhaps we should notice in this connection a general reduction in number of separate gill-filaments. In *Ecdyurus* there are very few such filaments, in little lateral tufts covered by shield-like scales which seem to be protective in design. Perhaps they are so in function: even in these swift reaches the current slackens among the stones, and drift-material may settle under them, against which these scales must be a valuable shield, while reduction of hairy fringes is convenient from this standpoint also, indeed, the general flattening of the body may bear reference rather to the habit of creeping for shelter beneath stones, where current is slight, than to actual current-resistance.

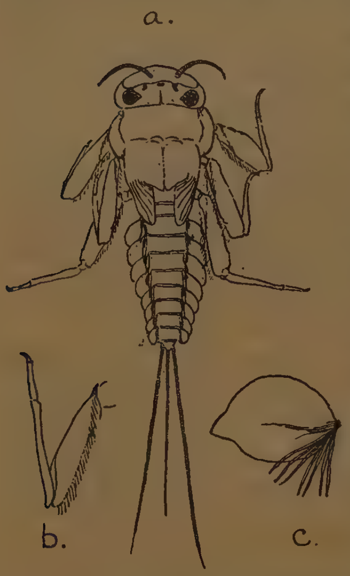

FIG. 64.—*a*, Nymph of *Ecdyurus* (? *lateralis*) from a swift brook. Note the general dorso-ventral flattening (enlarged about $2\frac{1}{2}$ times); *b*, one of the second pair of legs; *c*, a gill-lamella and tuft of the second pair.

The shelter of the stones is utilised by many other types of animals, most of which have some special adaptation of body-form which helps them to take advantage of it. Some rely for retention on a broad, smooth surface, mucus-coated, and fitting intimately into irregularities of the stone; the best examples of this condition are the brook Triclads: *Planaria alpina* and *Polycelis cornuta* may both be found in Highland brooks, and other species, such as *Pl. gonocephala* and *Dendrocœlum lacteum*, more characteristic of the lower reaches, may penetrate so far. In a Welsh area by far the most common form is *Pl. albissima*, a Triclad species first described from finds in Bohemian brooks, whose distribution is little understood.[8, 11] A similar method of adhering to the stones, in

essence, is that adopted by the few small Gastropod Molluscs found in these brooks; the organ of retention in this case is the broad sole of the foot, which muscular resistance to the action of forces of dislodgment converts into a functional sucker. *Ancylus fluviatilis*, the brook-limpet, is the most usual species; *Limnæa truncatula* is fairly common, and one or two others—as *L. ovata* and *L. pereger*—may occur. Species of *Hydra*, both *H. fusca* and *H. viridis*, use the aboral disc in the same fashion, and these are very common under stones in rushing brooks, although we are accustomed to think of them as pond-dwellers.

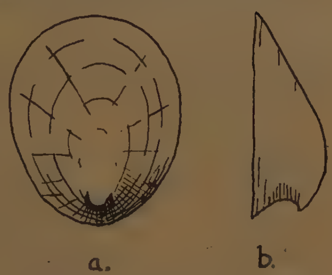

FIG. 65.—*Ancylus fluviatilis*, the Brook-Limpet. *a*, Dorsal view; *b*, shell in profile. (Usual length about 5 millimetres.)

Some brook-types carry this principle of adhesion further, and develop true suckers for attachment. Perhaps the most beautiful example of such forms is the flattened larva of a Dipteran, *Liponeura*, which has a row of six such ventral suckers, but no less efficient organs of adhesion are the two suckers (oral and postero-ventral) of the leeches. *Glossosiphonia* and *Helobdella*, in particular, are often found clinging underneath the stones. It is particularly interesting to find this use of suckers extending to the Vertebrates: fishes and even tadpoles of toads and frogs in mountain-brooks of South America and India have suckers formed by the lips or on the flattened ventral body-surface, which serve a similar purpose to that of the suckers found in our Invertebrates.[12] Some fishes use a different mechanism: Anabantoid fishes of the Himalayas wedge themselves among the stones by their movable spines, and the East Indian globe-fish (*Tetrodon*) has the most wonderful device of all. It creeps between the stones until it finds good cover, and then inflates its body, like a porcupine-fish, into a balloon-like shape which is so firmly wedged in that the current cannot dislodge it.[13]

A little Dipteran larva, *Simulium*, which congregates in

millions on the tops of stones in rapid water in our streams, holds on by a posterior sucker only, and lets its body stream out, head-foremost, with the current. This seems a dangerous habit, but the larva can also creep, using alternately its sucker and a curious hooked organ formed by amalgamation of a pair of legs; as it does so, it secretes from its salivary glands a fluid which quickly hardens to a silken thread, and usually the stones become coated with a network of such threads. If the creature falls, it trails a rope behind it, and climbs back to safety over its own threads, catching them in the prothoracic hooks (see Fig. 15, p. 40).

FIG. 66.—*Liponeura brevirostris.* A, Larva, ventral aspect, showing adhesive suckers; B, pupa, ventral aspect, showing adhesive suckers (after Steinmann).

Some other members of the torrent-fauna make a more systematic use of silk to weave loose shelters in the chinks and crannies between the stones: especially the larvæ of certain caddises. *Rhyacophila* has a large green larva with conspicuous tufted gills and a pair of slender, leg-like, posterior appendages with strong hooked claws, which crawls about the stones of highland brooks, spins threads irregularly, like *Simulium*, and uses its strong curved back-hooks to hold by them on to the moss, but many Philopotamidæ and Polycentropidæ make real shelters out of their threads. The most striking in its habits is *Hydropsyche*, the "spider of the rapids," which makes its lair far out into the current, among bare stones (see Chapter II); *Glossosoma* and *Polycentropus*, which makes a funnel-net, rather prefer mossy undersides, and *Plectrocnemia* is most often found in rather quiet eddies, among Alga-filaments. These types differ from

the case-building caddises in the leg-like form of the back-appendages, with their strongly curved claws for holding.

Case-builders in these reaches often make economical and effective use of bottom-materials, forming stony cases which shield their tenants well. *Stenophylax* and *Mesophylax* are the most common of Limnophilidæ, but *Anabolia* may sometimes be found, and often here deserts its usual habit of building soft cases of bits of bark and leaves, and utilises stony fragments.[14] *Brachycentrus* uses the under-stone drift of vegetable fragments to build its beautiful little four-sided case, which it attaches by silken threads to the top of a boulder, facing upstream. Some other caddises seem to build their cases on designs which are especially suitable to the torrential habitat: *Agapetus* makes a flattish pebble-case of relatively enormous breadth compared with the girth of its tenant, and with a smooth and gently concave under-surface which presses well against the stone substratum. *Silo* and *Gœra* also make flattened cases, but of less internal diameter, and fasten larger pebbles to their sides, making wing-like expansions which increase their contact-surface and at the same time act as ballast against the dislodging force of the current. *Apatania* builds a conical pebble-case, ventrally flattened, which it often fastens into stone-crannies by means of silken threads (see Fig. 59). Many more caddis-larvæ with quite delicate cases, such as *Tinodes* and *Micrasema*, find ample shelter in the crannies, owing to their small size, and protection of the

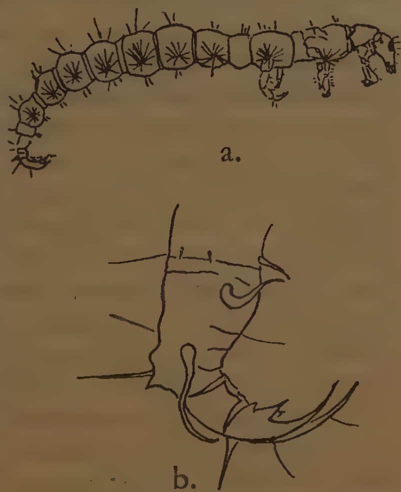

FIG. 67.—*a*, Larva of *Rhyacophila obliterata*, from a Welsh brook (about natural size); *b*, enlargement to show the strong posterior claws and hooklets.

same sort may be sufficient for soft-bodied, small, worm-like larvæ, such as *Tanytarsus*, *Orthocladius*, and *Cricotopus*.

The stones are used by many animals for sheltering the young in early phases of their development. Some water-mites lay eggs upon the moss, but others come to place their oval, flattened eggs in masses under the stones; cocoons of some Planarians lie freely in their interspaces, but *Pl. gonocephala* carefully attaches them, as do some leeches. *Herpobdella* makes beautiful oval, limpet-shaped cocoons of horny-drying secretion, firmly glued flat on the stones. *Limnæa* and *Ancylus* fix jelly-like masses to the pebbles, and all the brook-caddises, even those with wandering larvæ, have fixed pupa-cases. *Stenophylax* and many others wedge the pebbly cylinders well among large stones, fixing them by their lower ends. *Rhyacophila* and *Agapetus* make large, roomy pupa-houses of small pebbles built firmly on a larger stone as floor. *Simulium* makes a shield-shaped outer case for its cocoon, and fastens it to stones. The trout and other fishes of these brooks usually spawn among the gravel beds in shallows, and their heavy "demersal" eggs remain upon the bottom among the pebbles. Those of the bullhead adhere to stones in masses, and sometimes the male parent scoops a special hollow for them, and remains on guard during their development.

The stones which strew the beds of these swift brooks are the central pivots of the life which they contain, and the lithophilous fauna dominates the whole biocœnosium, although the moss tufts also play no small part, sheltering types similar to those found in them in head-streams, and also many of the lithophilous species in their young stages; the *fauna hygropetrica* is also developed in these reaches, though less strongly.

The life of the trout-beck, thus rapidly summarised, must now be considered from a rather different point of view. Besides those structural adaptations which enable its denizens to take shelter from the current, the animals, of so many diverse groups, have much in common physiologically: they have a common type of general behaviour. This finds expression very noticeably in the scuttle for shelter which ensues

when we disturb them in their lurking-places. Turn over a stone at the water's edge, and its clinging fauna, just now quietly resting in obscurity, promptly remove themselves into fresh shelter; disturb the bullhead, and he dashes off to hide beneath another stone. The stimulus which drives them is not blind panic, but something far more positive in action, as we may see if we bring some of these little creatures out of their retirement and place them in an open tank, leaving them undisturbed; they usually begin at once to move about restlessly, and so continue until they come at last to a full stop in the most obscure corner of the tank. Avoidance of strong light is perhaps the most marked feature of their behaviour: the animals of these torrential reaches are "lucifuge," almost without exception. One marked exception is the freshwater limpet, so often found in nature clinging to the upper surface of its stone; and *Limnæa* seems only very weakly lucifuge. All the under-stone clinging and sheltering types are strongly so in direct light, but some of them prefer light of a very low intensity to total darkness.[15] This light-avoidance is certainly a strong factor in determining their choice of sheltered situations. Another potent factor seems to be a tendency to take up positions in which the body, or some part of it, is in close contact with some other solid. This reaction—called stereotropism, or thigmotaxy—has been clearly demonstrated in the case of Planarians, which show a positive stereotropism of the ventral surface (the usual clinging side) together with avoidance of such contacts over the dorsal face[16]; a combination which clearly explains the adoption of the usual position with regard to stones. Many stone-clingers seem to have a preference for contacts: larvæ of *Ecdyurus*, *Isogenus*, etc., if deprived of stones for attachment, often group themselves in clusters, the smaller clinging to the larger, though the latter do not appear to relish the contact when it affects their dorsal surfaces; small *Limnæa* will behave in the same way. Shelford has shown[15] that many unrelated types of animals which live under stones in nature select this type of situation in preference to others, in a tank. Though it is always very difficult to analyse the factors in behaviour,

probably this one is almost as important as avoidance of strong light in this set of animals.

If we lean over the bank of a clear stream and watch the trout below, we notice that they always take the same position, lying along the line of the current and facing towards its source: if startled, they will always rush upstream. This tendency is shared by nearly all stream animals: *Asellus*, *Gammarus*, insect-larvæ, snails, and many others, taken from a brook and placed in an experimental current, move towards its source. This " positive rheotaxy " is the means of keeping the brook-fauna to its natural confines; if they turned in the reverse direction, the current would have full play to sweep them far away downstream; as it is, for many of them, like Alice, " it takes all the running *they* can do, to keep in one place." The nature of the stimulus which dictates their orientation has been the subject of discussion. Certain experiments carried out on fishes would seem to indicate that in the case of some, at least, perception may be visual, of moving objects carried past them by the current, since in still water they can be induced to move in a direction opposite to that in which dark objects are drawn past their tank.[17] Further observations on fishes and other animals are needed; the facts mentioned do not explain the maintenance of position in the dark. Probably some function of the static organs is at least partially responsible for the perception of the current-stimulus. Another stimulus which must induce movement in the upstream direction rather than the reverse is that supplied by the diffusion of food-particles along the current; chemotropism towards weak solutions is especially marked in all species of *Planaria*,[16, 18] and probably further researches will establish its importance in dictating the movements of many other aquatic animals.

Tropisms, or " forced movements," such as these just described, are of immense importance in the lives of lower animals; their combination, under the action of stimuli naturally in force, results in a consistent type of general behaviour which, without the need for choice, places the animal in those surroundings which are best suited to its

maintenance of life. Their exhibition depends to some extent on physiological condition : Allee has shown that some stream animals, after a sojourn in still water, cease to exhibit positive rheotaxy,[19] and in some Planarians the typical reaction is reversed if the water-temperature be altered or a chemical solution introduced.[20, 18] Without any physiological depression, the working of one factor may at times drive against that of another,[18] and in such cases the tropism may appear to be reversed or greatly modified ; it is the sum-total of such reactions, whose forces vary in relation to external and physiological conditions, that make up involuntary behaviour as we notice it.

Every naturalist knows how difficult it is to keep alive in an aquarium animals whose home is in swift brooks : their high mortality is generally attributed to dearth of oxygen, and certainly the oxygen-demand of most stream-species is very high, though readily supplied in the swift water of their native haunts. Many species are best kept in shallow water, which readily renews its oxygen in contact with the air, but some will never thrive even in carefully aërated water, unless it be kept moving. Such constant motion is essential, in many cases, for the sake of keeping the breathing-organs free from contacts and bathed by fresh water : caddis and mayfly nymphs with tufted tracheal-gills, and Agrionid larvæ, in still water, maintain a constant waving motion of the body, which shakes free the gills and enables them to function. Net-spinning caddis-larvæ of the rapids, kept in still water, cannot shape their snares accurately, but produce a muddled mass of threads without definite orientation.[21] In a wide, shallow tank, through which a current can be localised along one side, stream-animals in general will place themselves in the path of the current (and facing up it), rather than in the less disturbed water. This preference is known as "rheophily." Another frequent cause of death to stream-animals kept in tanks is their exposure to unusually high temperatures. In their native haunts, the water-temperature, as we have seen, is pretty constant and always rather low, and all the typical brook-fauna are physiologically low-temperature stenotherms.

It is a difficult task to separate these preferences, or demands, for low temperature, moving water, and copious oxygen-supply, and to decide the part which any one has played in fixing the habitat of a species; rheophily, though it may be absolute and independent in some species, may yet be only secondary in others to a demand for copious oxygen or for low temperatures, both of which a swift current helps to maintain. Again, low-temperature stenothermy may be fundamental, or itself secondary to the oxygen demand, since water at lower temperatures can hold larger amounts of gases in solution. Much interesting experimental work remains to be done in estimating these values for different species. Sometimes a study of geographical distribution may give a useful clue, as in the case of *Planaria alpina*, which seems in most localities to be fundamentally rheophilous and "poly-oxybiontic": its occurrence in the still waters of Alpine lakes fixes stenothermy as the fundamental factor, the rest being secondary, perhaps incidental. It may be noted, by the way, that recent research has shown that this and its fellow Ice-Age relict species (*Pol. cornuta*) differ from most of the torrenticoles in exhibiting definite *negative* rheotaxy: in their case, one factor which prevents them from straying into lowland reaches is a marked avoidance of high temperatures amounting to a negative thermotropism.[24]

Another question, which must be briefly dealt with, is that of maintenance of food-supply in the trout-beck. It follows from the lack of copious flora and of all plankton that the benthic fauna must be by no means over-fed. Many of them are microphages, and frequently current-feeders, like *Hydropsyche* with its web-snare, *Simulium* with its winnowing-fans (see Chapter II), and *Brachycentrus*, which spreads its bristle-fringed legs to sift the current. Decaying leaves and other organic material, drifting into the brooks from the dry land, may form a great part of the staff of life, supplementing the scanty home-production; even so, the brooks support a wealth of animal life which seems out of all proportion to the food-supply. The explanation probably lies in the prevalence of low temperatures, which retard metabolism, and the sluggish

life of many lithophiles, which, as Steinmann says, are usually half asleep; "he who sleeps, dines," is a maxim true enough within its limits. Certainly it is matter of common experience that most stream animals are able to endure long periods of fasting: an extreme case is that of Planarians, which can live for many months without a single meal, dwindling in size but apparently continuing to be healthy. When a meal does present itself, these animals, like leeches, gorge themselves, making full use of opportunities which do not come their way too often. One of the easiest methods of collecting Planarians is to place a dead frog, or a piece of raw meat, in the brook as a bait; a drop of blood, falling in the laboratory-aquarium, attracts a crowd of them to suck it up, and observations of this kind may hint at the importance of accidental treasure-trove to the carnivores of the brooks. Steinmann believes that nymphs of brook Ephemerids and stoneflies, facultative carnivores with strong biting mouth-parts, as well as the Planarians themselves, are omnivorous in practice, from necessity.

This same authority, in his classic study of mountain-brooks, observed a lack of seasonal changes in their life: most of the species were present all the year round, younger and older stages side by side. In his type-area, the temperature-range, as shown above (p. 138), was very small indeed; on lower ground the range extends a little, but the animal species are identical in many cases, and in the Sauerland Thienemann has found that the generalisation of the older worker does not hold good. The life of these brooks is seasonal in high degree, but its peculiarity is that the seasonal aspect is reversed from that of the pond-fauna, which attains its maximum development in summer. Precisely similar observations have been made in British streams, from rather lower levels to above 1000 feet: from late June to autumn (late September or October) the brooks seem almost empty of their fauna—a serious matter for the average worker, whose time of greatest leisure for collecting is in the long vacation! Collections of almost every species are best made in winter and in early spring, before the season of pupation and emergence of insects.

There is no "winter-sleep": food is equally abundant all the year, or perhaps rather more so in the winter, when the streams often flood and gather débris, much of it edible. Probably this plentiful supply in winter, hastening the phases in larval growth, accounts for the very early emergence of many insects from the brooks. *Simulium* and *Dictyopteryx* take wing in February from the Welsh streams, and from this time on throughout the months of spring the aquatic fauna continues to deplete itself; the numbers are restored in autumn when the summer's layings are hatched and the larvæ grown to appreciable size. One special seasonal phenomenon of peculiar interest is the alternation of sexual reproduction with summer-fission in the relict Planarians.[8]

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CHAPTER VII

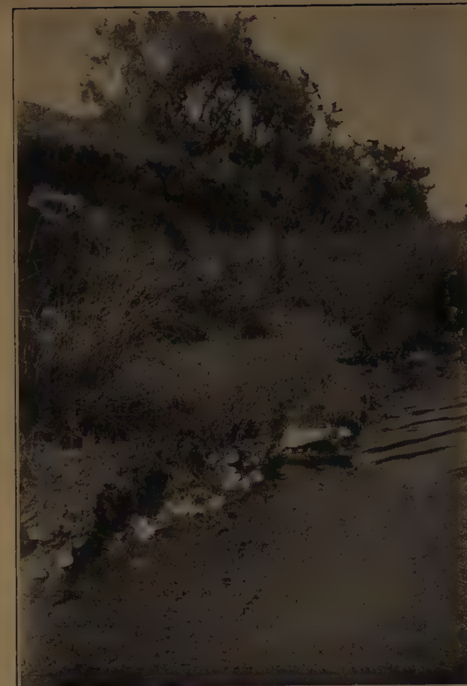
THE BIOLOGY OF RUNNING WATERS (*continued*): MINNOW-REACHES AND LONGER RIVERS

"And first concerning rivers: there be so many wonders reported and written of them, and of the several creatures that be bred and live in them, and those by authors of such good credit, that we need not to deny them an historical faith."—IZAAK WALTON.

A3. The Minnow-Reaches.—The trout-beck, with its rapid current and stony bed, passes insensibly into a succeeding phase of slighter gradient, slackened current, and less violent erosion; even here and there, in places where some obstacle causes its course to swerve, it may deposit scanty material, usually of coarse grade. The filamentous Algæ, such as *Cladophora*, which readily establish themselves upon the stones in moderate current, hold up the drift of decaying plant-material swept down from above, and in such spots true sedimentation soon begins to follow. Such stream-loving plants as *Callitriche* and *Ranunculus fluitans*, Water-Starworts and Crowfoots, may find a footing, and when once they do so silt steadily accumulates about their roots, where their own falling leaves mingle with it to produce a soft substratum. Frequent occurrence of such quiet places near the banks, as well as a rich growth of *Fontinalis* on the stones, is the signal mark of the establishment of that third phase in the life of a stream which we may call the minnow-reach. This corresponds in practice to the *Thymallus-zone* of continental workers,[1] but, as the grayling (*T. vulgaris*) is by no means general in its occurrence in our British streams, we choose to characterise this reach by the presence of a more common fish, *Phoxinus phoxinus*, the little minnow of the clear-running

PLATE
IV

IV*a*



IV*b*

(*a*) The minnow-reach of a Welsh stream. The shingle beaches have an abundant lithophilous fauna, while the growth of aquatic Phanerogams beneath the convex bank and in the stream (*Callitriche verna*) shelters a variety of phytophilous types, especially *Gammarus pulex* and Limnophilid caddises.

(*b*) A nearer view of the tufts of *Ranunculus fluitans* (just coming into flower) beneath the convex bank.

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brooks, which spawns among their gravel shallows. We might have named the zone after the salmon (*S. salar*), which ascends to it to spawn, preparing beds of gravel by the sweeping action of its tail, and covering the large, heavy-yolked eggs with sand and grit; but, since the salmon is not a native here, the minnow serves us better as a type.

Although the average current is less swift, and water-temperatures vary rather more, the stream is still a lively one, and oxygen-values well maintained, so that a large part of the torrenticolous fauna extends from the trout-beck into this reach. The only types which we can say with certainty do not inhabit it are a few proved glacial relicts of very rigid stenothermy. *Planaria alpina* does not extend its range so low; *Polycelis cornuta* is, in some streams of the Welsh area, a characteristic form during the winter: in summer it retires to higher levels,[2] repelled, no doubt, by rising temperatures. Another typical denizen of the trout-beck, the trout itself, is often to be found in lower reaches, but always retreats up-stream in winter for the spawning season.

With the development at the stream-side of peaceful, weed-grown shallows where the temperature varies in closer relation to the atmospheric readings, comes in a very important animal community, or group of communities, namely, the phytophilous, limnophilous and free-swimming eurytherms. *Gammarus*, and more especially *Asellus*, which found but little shelter in the closer mossy-tufts of the upper reaches, are quite important here, and in young stages still shelter in the moss.

A crowd of insect-larvæ congregate about the *Callitriche* tufts. Limnophilid caddises feed here, and species like *L. decipiens*, which makes its cases from the leaves of this plant, and nymphs of Agrionid dragon-flies (as *Enallagma*, *Ischnura*, *Platycnemis*) often cling to its fronds, while *Hydroptilidæ* fasten their little cases to the leaves with silken threads. The ram's-horn snail (*Planorbis*) and the pond-Planarian (*Polycelis nigra*), and larvæ of swimming beetles of the pools find shelter in the tuft or at its base among the sediment, which is the home of many other types. The little caddis

Micrasema minimum and several of the Leptoceridæ, which make curved cases of fine sand, cluster about the roots, to feed upon decaying fragments, with many species of *Limnophilus* (see Fig. 71). Little water-mites, as *Hydrarachna*, *Limnochares*, move over the sand in quest of living prey, small Cyprids often crawl on it (*Candona*); Tabanid larvæ haunt the gravel banks, and the finer bottom-sediment harbours quite a crowd of burrowing animals. *Ephemera*, *Sialis*, and Oligochætes, like *Naïs* and *Tubifex*, and the worm-shaped larvæ of *Chironomus*, *Tanypus*, and other such shelter in it or make loose tubes that lie upon its surface. Pea-shells (*Pisidium*) are fairly common here, and also the adaptable *Limnæa* (especially *pereger* and *auricularia*) and the bladder-snail (*Physa*), with its sinistral polished shell.

FIG. 68.—Acephalous larva of a gad-fly (*Tabanus*), found in river-gravel (after Brauer).

In these pools for the first time we may find a swimming insect population: *Dytiscus*, the great diving-beetle, is quite common, and even more so are its smaller cousins, *Hydroporus*, *Deronectes*, *Platambus*. *Corixa* and the minute *Sigara* swim in the lee of the plant-shelter, and *Velia currens* and even *Gerris* are often seen upon the surface film in the quietest situations, close inshore, occasionally even the whirligig *Gyrinus*. The plankton types still fail, but a few littoral species of *Cyclops*, such Cladocera as *Chydorus*, and *Canthocamptus*, always a phytophile, are found among the plants. Besides the swimming Coleoptera, small Hydrophilidæ and Parnid beetles are often found in plants, especially among the moss that grows on roots of trees that jut into the water. *Elmis* and *Helophorus* have several species in these brooks, but *Anacæna globulus* is the beetle most common here, particularly among the filaments of Algæ. In shallow, sandy pools the "niners," *Ammocœtes* larvæ of brook-lampreys, are sometimes found, half-buried in the sand.

The world of life within these little pools is a far richer one than that of the current. Here is no scarcity of food, except perhaps in winter, when the vegetation does to a great extent die down, only the moss and algæ remaining in abundance. The life of the pools is largely seasonal, since water-temperatures are more variable than in the stream itself, and in them the season of thin population is winter, when many of the animals disappear altogether, while others, like *Dytiscus*, *Corixa*, and *Velia*, partially hibernate in mud or under banks, but may wake to activity on days of sunshine.

FIG. 69.—*Anacæna globulus* (after Brauer). Actual length 2–3 mm.

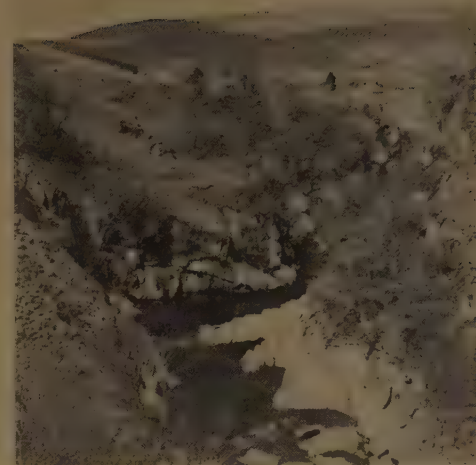
The minnow-reach is the transition-stage between the trout-beck, with its torrenticolous fauna of low-temperature stenotherms, and the lower river with its population of eurythermous types; the reach itself is peopled by both these stocks, presenting the strongest possible contrast to one another. The torrenticoles number among themselves not a vast crowd of species, all told; their distribution is constantly related to the presence of cold stenothermous waters, whether in mountainous regions, or in the far North, or in the reaches just below cold springs. Most probably, as Steinmann has maintained,[3] they represent *en bloc* survivors of the Great Ice Age in Europe, forced to retreat to these high reaches and there to adapt themselves to resist the driving of a current which, though it brings some perils, brings also copious oxygen and low temperatures, so that it is to them a life-giving force. The animals of the quiet waters of streams are typically eurythermous cosmopolitans; their distribution is broad and regular, and their adaptability immense. The lower temperatures of the torrent-reach are probably in themselves no barrier to the upward extension of this fauna: what does prevent it is their lack of adaptation to resist the current, coupled with a food-scarcity which only barely permits the old-established fauna to maintain a footing in the higher courses.

B. The Lowland Courses

The biology of plain sections of rivers has been less carefully studied than that of highland brooks; in Britain we have as yet no collected data, and even in other countries where freshwater studies are more advanced there is a certain dearth of river-surveys.[4] The dominant features of the lower courses are increase in the volume of the water and slackening of its current, with a greater variability of temperature and a tendency to deposition of material rather than erosion. This comprehensive statement of general type is permissible, and even necessary, but it must be remembered that there is infinite variety among the separate rivers and from one locality and even one season to another in a single stream. Rivers with many head-streams draining an area of heavy precipitation will have the greatest speed and volume; rivers which flow over a country rock of granite or Palæozoic strata will usually have least sediment; extensive glacial deposits, as in a great part of the Baltic area, condition the turbidity of streams. Rivers which draw from snow-covered highlands will be subject to violent floods in spring, when water, clouded with suspended mud, comes rushing from the hills. Flooding may alter levels very seriously even in the spring-fed rivers of a temperate country, and usually in summer the river stands a good deal lower than its winter average. The current is not uniform throughout the river in cross-section: it is swiftest near the middle of the stream, as friction holds it back along the sides, but where the river loops the current may impinge quite sharply on the convex shore, eroding violently, while along the opposite bank the shallow slack-water deposits sediment. In times of flood the increased carrying power may bring down quantities of gravel and even coarse pebbles into the lower reaches, to be deposited in flood-banks which materially alter their topography and influence the life within them.

We must acknowledge the grave difficulty of arriving at any precise data applicable to the biology of rivers as a whole:

PLATE
V



Gorge-section of a Cardiganshire stream. Only a very scanty lithophilous fauna can find precarious foothold on the rocks swept by the rapid current. The reach is almost barren of life.

To face p. 164.]

the best that can be done is to formulate those broader features in which it differs from that of the reaches above, which we have studied.

Two factors seem to us to be supreme in their importance. The first is temperature-variation, which follows the daily average atmospheric-readings in rather the relation borne by the track which the hind-wheel of a bicycle makes in the sand to that drawn by the fore-wheel—keeping the general course, but smoothing out the sharpest turnings.

This variation definitely shuts out the stenothermous torrenticolous fauna from large lowland rivers in a temperate climate: this fauna is the "brook-fauna" *par excellence*. The second class, the eurythermous cosmopolitans, which we found already winning a way to establishment in quieter patches of the minnow-brooks, is universal in its dominance of river-courses proper, and attains here to far greater richness and variety of species than above, though similar elements are represented. Especially, there is substitution and increase of the Molluscan species; the little pea-shells were the only typical Lamellibranchs in the brooks, but in these waters we find their giant relatives, the freshwater mussels. In British rivers we have species of *Unio* and *Anodona*: the latter ploughs its way through bottom-mud, but *Unio* is more common in clear shallows, where the pearl-forming species, *U. margaritifer*, is sometimes found. Among Gastropods, *Limnæa pereger* and *L. auricularia* may be important still, *L. truncatula* never; *Planorbis* has more species here, especially *P. corneus*, the diameter of whose coil may span an inch—twice that of any found in highland brooks (see Fig. 19, p. 43); and a new genus, *Paludina*, the freshwater periwinkle, is found in slow waters of some British rivers.

The case of the Mollusca has been taken as an illustration of the general principle that in the lower rivers species dependent on the presence of fine-grained bottom deposits, with plant growth, are relatively common. Given the eurythermous character of the fauna, the dominant factor in the life of lower rivers is the character of their sediments. There is another aspect of the question of bottom deposits: though they give

protection to burrowing forms and anchorage for plants, and often in their surface layers hold valuable food-material derived from decay, yet the phase of their actual deposition is by no means the most favourable for establishment of any life. Seeds and young plantlets growing in river-beds are sometimes buried under layers of sediment which, if fairly coarse, may injure them mechanically, if too fine, cut off the necessary light and oxygen. The mere turbidity of water is a serious factor in retarding growth of plants dependent upon sunlight for carbon-assimilation, and, besides lessening the food-supply of animals, exposes them to dangers worse than those incurred in pebble regions, because more insidious: the clogging of breathing and locomotor organs by films of mud. Therefore the life of rivers of the plain is concentrated in their quiet pools, where only a faint deflection of the current deposits finer sediment so slowly that rooted plants can take their stand in it and, binding it together by their fibres, establish the beginning of a community which is in essence not proper to running waters, but of lenitic character. The flora and fauna of the river-pools, especially of backwaters which are left aside from the main channel in its windings over a level plain, are little different from those of ponds. Phanerogams flourish here: *Œnanthe*, *Sparganium*, *Hippuris*, *Elodea*, *Zanichellia* and even *Myriophyllum* replace the lovers of swift waters; even *Potamogeton*, *Lemna*, and water-lilies may spread upon the surface in backwaters. Dominant associations among animals are phytophiles and all but the lithophilous benthic types.

In sandy and clayey banks of lower rivers, burrowing larvæ of Ephemerids make horizontal tunnels; these mayfly warrens cover great areas in some rivers, and number their inhabitants by myriads. The burrowing nymphs are easily recognised by the enlargement of their first thoracic legs into strong digging organs, with which they shovel out material, throwing it behind them like a tunnelling mole (see Fig. 45A, p. 93). *Polymitarcys virgo* makes its burrows U-shaped and open at both ends, for convenience of separate exit and entry, and lines them with a layer of finer particles than those of the

clayey bank[5]; *Palingenia* also prefers clay-banks,[6] and so does *Ephemera vulgata*, but *E. danica* seems to be limited by its weaker powers of digging to sandy beds.[7]

The burrowing habit serves those animals which adopt it in several obvious ways; most obviously, it affords protection from enemies too large to penetrate the burrows, and not sufficiently strong or cunning to tear them open. Second, burrowing is in the end economy of action for stream animals; the expenditure of capital energy involved in digging brings in its interest in the shape of opportunity to rest in shelter. Lastly, the tunnels, being firmly made, and often carefully lined with a resistant layer, insalivated or well kneaded together, shelter the animals against drifting or settling particles of that very material in whose accumulations they are formed. This turning of adversities to profit reminds us of the similar use of stone-shelters in torrential brooks. But burrowing has its drawbacks, for aquatic animals in particular; it generally involves adoption of the microphagous habit, reduction of individual size, and loss of powers of rapid locomotion. If accident or the cunning of an enemy destroys the burrows, their tenants are unprotected, and, unable to make a rapid escape, fall wholesale victims to their enemies. The most successful of freshwater burrowers, which have retained their powers of rapid locomotion and great bodily strength, are the crayfishes of the sandy banks: *Astacus*, in British streams which draw from chalk, *Cambarus* in America, and other genera further afield. In rivers with muddy, shelving bottoms, small Oligochætes, as *Naïs* and *Tubifex*, may reach enormous numbers: in the Lower Elbe, near Hamburg, Hentschel found in a stretch of soft bottom 10 metres square over three thousand *Tubifex*[8]; tube-forming Chironomids may outnumber these, and pea-shells often run them fairly close. About the roots of plants, small Nematodes are found, and Entomostraca of littoral habit (*Acroperus leucocephalus*, *Cyclops fimbriatus*, *Canthocamptus* . . .) and Rotifers (as *Brachionus spp.*) are frequent in proportion to the stillness of the water.

Spongilla (*Ephydatia*) *fluviatilis* is a very characteristic form in rivers with clear and not too rapid courses, where it

forms green incrustations on banks or floating timber. A little movement of the water gives excellent opportunities to current-feeders, but for all sedentary types the silting danger is peculiarly acute. We seldom find *Hydra*, for instance, in the lower rivers: it is a common type in brooks and ponds, and rapid streaming or a quiet life seem all the same to it, but turbidity of water is a peril which it avoids. Only in quiet backwaters, where the presence of *Lemna* and *Potamogeton* bespeaks the pond-like milieu, we may find

FIG. 70.—*Ephydatia* (*Spongilla*) *fluviatilis*. A, Encrusting type, found in running water and on wave-washed littoral; B, branched type, found in still water.

Hydra, *Vorticella*, and a number of other Infusoria, sedentary and free.

So far we have made no mention of the life by which the lower reaches of a river are perhaps most definitely characterised: the nekton of the swimming fishes. This is very variable from stream to stream in Britain, but we notice the predominance of members of the Cyprinidæ, or carp family. This is perhaps the largest order of free-swimming fishes, and its members, being characteristically more active in the warmer season, and breeding in late spring or early summer, stand in

PLATE VI

(*a*) Plain-section of a long river, in the zone of dominance of Cyprinid fishes. The muddy banks are fringed with willows, and the limnophilous fauna is well developed at their bases.

(*b*) Brackish-water reach of a Cardiganshire stream. The shingle bank on the right is a storm-beach thrown up by the sea at high tide; the splash-rings behind and to the left of this were made by brook-trout leaping for mayfly (8.30 p.m., June 1, 1928).

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sharp contrast to the cold-loving Salmonidæ of the upper reaches. Our carp, the typical members of the family, although they fare so well in European waters, are not indigenous, but have been introduced from Asia, and the whole family is probably of southerly origin. The oxygen demand of the Cyprinids is far below that of the trout and salmon, and their tolerance of ill-aërated waters is extended by their faculty of gulping surface-air when the dissolved supply falls low. The air-bladder of these fishes retains open communication with the gullet, and undoubtedly the organ serves in gaseous respiration, a function very valuable to fishes which frequent the muddy reaches. Extreme development of air-breathing organs is seen in other fishes, such as *Polypterus*, which live in swamps (see Chapter III). Most of our Cyprinid fishes retire in winter to the shelter of some mass of weeds, or even into the mud, and remain there in a half-torpid condition. Carp never feed in winter, and the tench (*Tinca vulgaris*) is said to attain a phase of torpor in which it can be taken from the water and freely handled without awakening.[9] Some of the smaller species are fairly active in the winter, and these usually frequent the upper parts of the Cyprinid reach in long rivers, or else clear lowland brooks; familiar species are the gudgeon (*Gobio fluviatilis*), chub (*Leuciscus cephalus*), dace (*L. leuciscus*), and bleak (*Alburnus lucidus*); the minnow, as we have seen, is found still higher in the streams. Characteristic fishes of the lowest courses are carp, tench, roach (*Rutilus rutilus*), and especially bream (*Abramis brama*), all of which are also found in ponds. All spawn in late spring or in early summer; the ova cannot be left on the bare bottom, as in the stony brooks, for want of shelter from drifting or silting, but as a rule they are shed in the neighbourhood of plants, to which they adhere in sticky strings or loose clumps. The little stickleback, which is very common in muddy ditches and near the mouths of rivers, goes further in the protection of the eggs, as we have seen (Chapter IV). These fishes feed on worms, freshwater shrimps, and insect-larvæ in great variety: such food is plentiful among the rich plant-growth of quiet waters. The

burrowing mayfly of the loose banks, though well guarded from raids while in their burrows, are an important source of food-supply. In early summer, when the final moult comes upon nymphs of the second year of life, the air above these lower streams is clouded at certain times with the swarming millions of the perfect insects. No better picture of their emergence and fate can ever be drawn than that of Réaumur, which every naturalist should read.[5] As any angler knows, the rising of the mayfly is the beginning of the happiest period in the lives of river-fishes, which have so little time to wait before the exhausted insects, having quickly fulfilled their racial duty of propagation, fall back, many of them to drift upon the water into the snapping jaws that await them. But this epoch of satisfied gluttony for fishes is also the time of their greatest peril, as, again, the angler knows.

Little information is to hand concerning the diet of young river-fishes, after the yolk-supply has been exhausted. The young of marine fishes mostly feed on plankton, and, although in highland reaches the swift current and small volume of the water preclude the presence of such floating life, the lower reaches of large rivers may contain abundant plankton. In the Illinois River, where the mean velocity of current varies from 0·6 to 2·572 feet per second, Kofoid found an average of 2·71 c.c. of plankton per cubic metre in the sum total of all the reaches studied, and calculated [10] that the annual discharge of plankton from this river at its mouth (*i.e.* over and above the quantity eaten or destroyed *en route*) was nearly 68,000 cubic metres. Kofoid's study of the plankton of this river is the standard of reference on a subject which had been for some time previous to his work (published in 1903) the subject of less systematic observations, and of a great deal of speculation.

Zacharias, studying the lower courses of some North German rivers,[11] observed the presence of a plankton especially rich in minute Algæ—Desmids and Diatoms; Rotifers (*Brachionus*, *Philodina*) were far behind these in frequency, but still greatly exceeded other animals in numbers. A mixed assemblage of such Protozoa as *Arcella*, *Difflugia*, *Stylonychia*,

Stentor, and *Coleps*, with a very few Cladocera (*Chydorus*, *Simocephalus*, *Sida* . . .), a *Cyclops* here and there, and an occasional *Chætonotus*, *Hydra*, or Turbellarian made up the tale. This early find is reported here in some detail, because it gave a valuable clue to the solution of the problem of the occurrence of plankton in rivers: how is it possible for floating life to be maintained in the presence of a current? Zacharias noticed that the river-plankton bore a suspiciously strong resemblance to that of ponds: the same rich development of Algæ of pond-type, with *Pediastrum*, the pond-star, *Melosira*, *Fragilaria*, and so on; the same species of *Brachionus*, *Polyarthra*, *Anuræa*, among the common Rotifers, characterised both, while the "occasional types" included littoral Crustacea, common among weeds, and forms like *Vorticella* and *Hydra*, which so often hang from floating plants. Zacharias prophesied that we should find the origin of the plankton of rivers in backwaters and still pools, aside from the main channels, though Diatoms might perhaps multiply in the stream itself.

Schröder and Zimmer,[12] working on the Oder, near Breslau, found a rich development of "potamoplankton" just below the reception of a tributary from a pond, and recognised many species as derived from the pond ("tychopotamous"), though Schröder was of opinion that some few of the Algæ were peculiar to the river, and therefore "autopotamous" in origin. The main mass of the plankton they found to be "eupotamous," having its development in the backwaters. Schröder was led to formulate a law of inverse proportion between the volume of plankton in a river and the velocity of the current, but factors are too complex for any such precision of relations. The monumental work of Kofoid, extending over several years of careful observations, showed clearly that the volume of the plankton varies from season to season, from day to day, according to such factors as (*a*) temperature of water in backwaters and main stream, (*b*) incidence of floods, which sweep it out in masses from its place of origin, and are followed by long periods of slow recovery from the check on production, (*c*) character of the

impounded areas: shallow backwaters, where rooted plants grow to luxuriance, produce most of the plankton, but a covering of floating leaves, such as those of pond-weed and water-lilies, shuts out the light and so impedes production. Geological character of the substratum, and influence of effluents from factories and town sewers, all affect plankton-production. When the river is low, the current being slower, the phytoplankton, able to continue carbon-assimilation all the time, may multiply considerably on the way towards discharge; the zoo-plankton cannot be expected even to maintain its numbers, far less to multiply, since solid-feeding must be difficult *en route*: this partially explains the predominance of plant-members in the potamoplankton. The fair frequency of Rotifers must be referred to the rapidity with which they multiply in the backwaters; also, they exhibit marked positive rheotaxy, and some of them can swim well enough at any rate to retard them considerably in the downstream passage.[13] The maximum of plankton in the rivers often occurs in early summer, as we might expect, when there is a high rate of multiplication in backwaters, but "plankton-pulses" of far greater frequency are very marked,[10] and these must be referred to interaction of the complex factors described above.

Not only are littoral types brought into the main channel by the sweeping action of the current, but also some small benthic forms may rise, buoyed up on oxygen-bubbles produced in carbon-assimilation by bottom-living Algæ. *Oscillatoria*, which often forms a felting on submerged mud, is frequently heaved up in this way in little tufts, bearing with it minute animals, especially *Arcella* and *Difflugia*, which come to join the plankton-population.[14] This element in the potamoplankton has been called "bentho-potamous"—but why multiply terms? Even the central term, "potamoplankton," is questionable in use, since, in the first place, many of its elements are not "potamous" (originating in rivers), and, again, many which are so and some of the remainder are not true planktonts. The potamoplankton can have no status as a biocœnotic entity, since it owes its origin

PLATE VII

VII*a*

VII*b*

(*a*) A backwater and (*b*) a "cut-off" pond in the lower valley of a Cardiganshire river. Both are fringed with *Juncus* and *Scirpus*, and the water is almost covered by the floating leaves of Potamogeton; both contain trout, sticklebacks, and an abundant phytophilous invertebrate fauna.

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to causes which, if too constant in action to be called *ac*cidental, are at least purely *in*cidental. Lauterborn, in his study of the Rhine,[1] shows how profoundly the fauna of the main river is influenced by the accession of types from the rich breeding-grounds of lakes and backwaters.

Sooner or later, all these adventurous wayfarers meet an untimely end, for " even the longest river winds somewhere safe to sea " ; increased salinities, with mingling of marine and fluviatile waters, must in the end prove fatal to all members of the freshwater population proper.

C. The Brackish Waters

The estuarine reach of tidal action, the scene of violent alternations of temperature, salinity, and force and direction of current, has its own peculiar life. A few freshwater species can resist these changes just sufficiently to enable them to spread, though in diminished numbers, into the tidal zone. Some little beetles (several species of *Hydrobius*, *Platambus maculatus*, *Deronectes depressus* . . .) and a few other insects (especially *Notonecta* and some *Nemura* larvæ) are the last to disappear ; as a rule, soft-bodied animals like Planarians, molluscs, segmented worms, and all Cladocera fade out quite quickly : probably rapid diffusion through the weak covering membrane is the cause. Some marine types come in, but as a rule the brackish waters have a special life, composed of " euryhalines," resistant to great changes in salinity. Some of its species are particularly interesting because they penetrate in certain localities into the true freshwaters : examples are *Paludestrina jenkinsi*, *Dreissensia polymorpha*, *Cordylophora lacustris* (see Chapter I). Some others are only found in brackish waters, but have near relatives inland, probably modified surviving immigrants. For example, *Gammarus duebeni* in brackish water, *G. pulex* in fresh—*Eurytemora affinis*, *E. lacinulata*, *E. hirundo*—have each its own appropriate range of salinity, and similar gradations of species of *Corophium* and *Acartia* have been observed.[16] The number of Crustacea to be found in brackish waters is particularly

high; in brackish pools quite cut off from the sea along some of our sandy coasts, *Palæmonetes varians*, *Neomysis integer*, and *N. vulgaris* are quite common, and may be in process of evolution here into freshwater forms, like the older Baltic relicts not too distantly related to them ([17] and Chapter V).

Most interesting of all the euryhalines are the wandering fishes, which can pass from sea to fresh water, and *vice versâ*, without suffering. Not many truly anadromous fishes visit our British rivers: among them salmon and sea-trout (*S. trutta*) are of course most prominent. The latter species is less regular in its migrations than *S. salar*, and may spawn close by the coast or in the estuaries: it never mounts more than a mile or two. A third migratory Salmonid species is the houting (*Coregonus oxyrhynchus*) of east-coast rivers. Smelt (*Osmerus eperlanus*) and "freshwater herrings," or shad (*Clupea alosa* and *C. finta*), also spawn in British rivers or estuaries, and the sturgeon (*Acipenser sturio*) of continental rivers may sometimes pay a fleeting visit to our coasts. The sturgeon of the inland lakes of North America is probably an anadromous type which has evolved into a lacustrine species after the manner of most *Coregonus* (lake whitefish).

The problem of the factors which determine the spawning migrations of fishes is one of great complexity. The case for supposing an hereditary tie which induces the return of salmon to the streams in which they breed, after a sojourn in marine waters of richer food-supply, has already been put, but we must not forget that many purely marine fishes, such as herrings, seek the inshore-waters at the breeding season, and anadromous types which penetrate some little distance up the streams may be obedient only to a similar physiological demand. An interesting suggestion is that the quest for waters of a less salinity, and, therefore, of lower specific gravity, may be dictated by discomfort due to the diminution in the body-weight occasioned by the copious deposition of fatty food-reserve in the tissues, just before the spawning-season. Another theory is that the increased rate of metabolism and a species of auto-intoxication due to

hormones secreted by the active gonads demand an environment in which the temperature is low and copious oxygen present in solution.[17] Certainly it has been observed that the Alaskan salmon, at the confluence of two streams, chooses that in which the temperature is lower. When once a fish is brought within the sphere of influence of a river, probably the usual positive rheotaxy will lead it to ascend against the current; but why do salmon seek the reaches so much further from the sea than other types of anadromous fishes?

The converse of the anadromous habit is the migration of the eels, which leave their feeding-grounds in muddy pools and broads to seek the open sea at spawning-time, a mystery only fully appreciated in recent years, which gave rise to the delightful theory quoted at the head of Chapter IV. The story of the eel, one of the most fascinating in natural history, cannot be told appropriately in a work concerned with life in the freshwaters; but we must mention that procession of the "eel fare"—myriads of little agile elvers, which make their way up from the sea in spring through estuaries and along the rivers, turning aside into the muddy ditches and ponds on the low ground. Cases are known of mature eels which, finding the inland situation too comfortable to desert, neglect their racial duties and remain celibate in the ponds, reaching a ripe old age and waxing to enormous size: the writer knows of one, aged about twelve years, whose landlord asserts that it comes at his whistle to receive tit-bits.

This comprehensive sketch of the succession of life in a long river, while it cannot apply in all its substance to every one, may serve as index for the biological classification of stream-reaches. This is a field in which much detailed work needs to be done. The life of lowland-brooks, intermediate in some respects between the trout-beck and the Cyprinid reaches, where there may be quite a rapid current from the springs, but sediment is often very considerable, owing to the softness of the valley floor—this ought to be studied especially in Britain, where we have so many of such brooks. One of their special features seems to be mass-development of Linnophilid- and Phryganid-caddises that make vegetable-

cases, as well as frequency of *Planorbis* species and certain Planarians, such as *Dendrocœlum*.

The question of the distribution of stenothermous species in brooks in lower areas presents a fascinating subject for research, in view of the alleged Ice-Age relict status of so

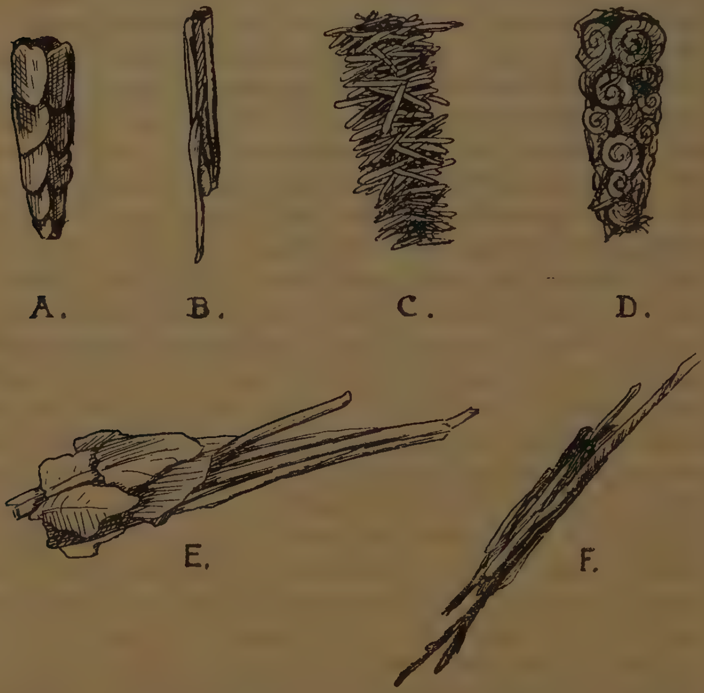

FIG. 71.—Cases of caddis-larvæ in slow-running brooks or standing water. A, B, *Limnophilus decipiens*, leafy cases; C, *Limnophilus rhombicus*, leaf- and stem-fragments arranged crosswise; D, *Limnophilus flavicornis*, case adorned with small shells; E, *Stenophylax infumatus*, case of leaves and straws; F, *Anabolia nervosa*, case of bark and twigs.

many of these species. In Britain very little work has been attempted on the Triclad Turbellarians, which include two of the best-established of relict species, *Polycelis cornuta* and *Planaria alpina*, but we have a few scattered records of these species from such low altitudes that doubt has been thrown upon their stenothermy.[18] It may well be that our more

PLATE VIII

(*a*) A lowland brook with rich development of rooted vegetation and phytophilous fauna.

(*b*) A Cardiganshire spring-brook. Though only fifty feet above sea-level, this rheocrene brook contains the Ice Age relict, *Planaria alpina*.

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moderate climate confers upon the lowland brooks a power to shelter stenothermous species which on the mainland belong to higher altitudes. The writer's study of the brooks of a hilly part of Western Wales revealed the extension of the torrenticolous fauna down to almost sea-level; these streams owed their stenothermy only in part to springs, and very largely to the rapidity of their courses, shortened by subsidence of a great part of the coastal plain since the Great Ice Age.

Careful records of temperatures and of faunal successions in British brooks of all types are greatly to be desired. In lower rivers the work is vast, and all of it still to do.

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CHAPTER VIII

THE BIOLOGY OF LAKES

"It is well known that in the Lake Léman, the Lake of Geneva, there are trouts taken of three cubits long."—IZAAK WALTON.

THE pioneer investigator in limnology proper was Forel, whose magnificent work on the hydrography and biology of Leman and other lakes of Switzerland laid the foundations for an immense edifice of scientific fact and theory still being raised about this complex topic.[1] A lake, considered as the home of life, includes within its bounds a great variety of habitats—in deep water and in shallow—in still and agitated—and so on; further, lakes vary greatly one from another according to their situation, origin, and history. To condense the vast material derived from innumerable separate studies in lake-biology into one brief summary demands the taking of a synoptic view which must needs be highly unsatisfactory from many standpoints. We can here do little more than indicate the chief divergent lines along which special studies may be pursued.*

At the outset, we may classify the regions of a lake into "littoral and benthic," on the one hand, and "pelagic" on the other.

* It will be only possible to give explicit references to a very few of the many separate papers bearing on the subject. Many more are to be found in Thienemann's volume *Die Binnengewässer Mitteleuropas* (Stuttgart, 1906), and many of the separate studies are to be found reported in the two series: *Archiv für Hydrobiologie und Planktonkunde* (Stuttgart, 1905 *et seq.*), and *Revue Internationale der gesamten Hydrobiologie und Hydrographie* (Leipzig, 1909 *et seq.*), as well as *Annales de Biologie Lacustre* (Bruxelles, 1906 *et seq.*)

The Littoral and Benthic Regions of Lakes

The general slope of the lake-floor from shore to middle-bottom, considered as supporting-ground for life, may be divided into several zones, which grade into one another as the environmental factors slowly pass from the unstable conditions at the outer margin into the uniformity which characterises the bottom region. Gradation is exhibited chiefly in respect of the under-mentioned characters :

1. *Movement of the Water.*—This is greatest (excluding the influence of special currents) around the margin of the lake, where winds affect the shallow water very sensibly. Wave-action usually ceases at about 10 metres depth.

2. *Temperature.*—In shallow reaches, water-temperatures vary in close relation to those of the atmosphere. At 12 to 15 metres in Lake Leman Forel found diurnal variations not strongly marked, but still discernible ; at a depth of about 100 metres, even annual variations disappeared, and temperature was stable to $\pm 0{\cdot}5^\circ$ C. round about the point of maximum density of water $+4^\circ$ C.

3. *Illumination.*—Light penetration varies very greatly in lakes of different types, and according to the latitude, seasons, and character of affluents (whether mud-charged, etc.), also according to the vegetation, which in its turn depends upon all the foregoing factors. In Lake Leman, where transparency is high, Forel found the maximum limit of penetration of actinic rays at 45 metres depth in summer (when waters were turbid, through the melting of snows and ice above), at 100 metres in winter, while the limit of distinct vision, and that of copious green vegetation, coincided pretty well with that of the diurnal variations in temperature.

4. *Pressure under Water.*—This of course increases with depth, but, as already indicated (see Chapter III, p. 73), it is probably of little importance in lakes as a biological factor.

5. *Character of Bottom.*—Bare rock and erosion-beaches at the margin range through sedimentary deposits of various kinds to the fine mud of deep waters.

The most clearly marked of all the zones from margin to

lake-centre is the *littoral*, or in-shore zone, which must be taken to coincide with the belt of abundant green vegetation which is so important in its bearing on problems of food, shelter, and solution-content of the water (see Chapter III). This zone was defined in Lake Leman as extending to a maximum depth of 20 metres. In lakes of northern plains, with gentle gradient, the limiting depth may be as little as 3 to 7 metres, but the loss in vertical extent is more than compensated by the gain in actual breadth along such sloping shores.

The lower zones are far less clearly marked. Forel made two great subdivisions, " upper and lower deep-water zones," in contact at a depth of 60 metres (the limit of annual variations in temperature). Modern workers usually prefer to recognise a " sub-littoral zone " [2] or " upper deep-water belt," [3] ending at about 50 metres in lakes of the plain type, with annual variations in temperature over a range of less than 3° C. round about 14° C., and below this a " profound " or " deep-water " region—though these may be still further subdivided. In European lakes, the series closes here, but in a few extra-European, as Baikal and Tanganyika, an " abyssal region," beginning at about 600 metres, and very peculiar in character, is recognised.

A. The Littoral Zone

This may have two main aspects at its margin: on the one hand, the open wave-washed shores—" erosion-littoral," or " Brandungszone " [4]; and, on the other, the gently sloping shore of the " quiet littoral."

Phase I.—*Erosion-littoral*

The water-level varies a good deal, not only with the seasons, but at shorter periods, owing to variations in wave-production due to wind. About the upper limit of water-levels a shore-community of land-living or amphibiotic types rather like that of the spring margins (Chapter VI) is also found; the true aquatic fauna mostly keeps back within the

PLATE IX

(*a*) Shore of Loch Ness from Glen Doe Pier. The rocky nature of the shore, together with the constant wash of the waves, prohibits phanerogamic vegetation in the littoral waters. (Compare Plate V.)

(*b*) Loch Bran. The belt of emergent vegetation (*Phragmites communis*) is followed by that of floating-leaved plants. ((*a*) and (*b*) are from West's "Flora of Scottish Lakes.")

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lower "tide-mark," and may best be studied at seasons of low water.

The dominant factor here is motion of the water: not a steady onward flow in one direction, such as we find in rivers, but constant turmoil, backward and forward dragging and thrusting of loose material—a very strong dislodgment force. Temperatures are certainly variable, but less so than they might be, in shallow water, because wind-action continually brings surface-water from the centre of the lake, whose temperature is more even, towards the leeward shore. Communities of this shore are of two main types:

a. The Stony-Beach Community

The presence of loose boulders and pebbles conditions here a scanty flora rather like that of brooks, with tufted Bryophytes, and particularly common on calcareous ground are Algæ like *Tolypothrix* and *Schizothrix*, which form encrusting growth upon the stones, and shelter a small fauna of tube-forming caddises (*Tinodes*), small beetles (*Platambus Laccobius* . . .), *Chironomus*, *Tanypus*, and sometimes *Gammarus*.[5, 1] This is the region of formation of those calcareous tuffs associated with the shores of certain lakes, which owe their origin to the decomposition of soluble carbonates by plant-activities, with deposition of the bicarbonate which settles in a crust about the stones; the crust is sculptured into grooves and tunnels by settlement of plants and animals.[5] On the stones of beaches round about the lakes of Scandinavia and many Scottish lochs, Diatoms are especially abundant.[6]

Among the stones, and sheltering under them, we find a type of animal community pre-eminently "lotic" in adaptation for clinging, in resistance to the force of waves. Wesenberg-Lund [4] first called attention to the superficial resemblances between this fauna, on the wave-washed shores of Lake Furesö, and that of torrential streams. Dominant types are stone-clingers; in Furesö, common Ephemerids are *Ecdyurus* and *Heptagenia*, both nymphs with bodies flattened dorso-ventrally in much the same way as the *Epoürus*

of Steinmann's mountain-brooks (see Chapter VI); the common stonefly here is a *Nemura*; the caddises are *Goëra*, *Leptocerus*, some Polycentropidæ, *Crunœcia*—all types common in brooks and well adapted to resist dislodging forces. Molluscs include species of *Limnæa*, *Ancylus*, and *Neritina*; *Planaria* and others of its tribe are very common, as are Clepsinid leeches, clinging beneath the stones, and on their surface *Spongilla* grows in singularly flattened encrusting masses (see Fig. 70, p. 168); *Gammarus* shelters in the mossy tufts. No one could fail to note the strong resemblance to the brook-fauna.

Workers in other districts find this type of community is characteristic of the stony beaches.[3, 7, 8] In plateau-pools in Wales, enclosed by artificial dams of loose quarried stones, the writer also finds it well-developed, and including many of the actual species characteristic of Welsh highland brooks. This very close agreement seems to support the original suggestion of Wesenberg-Lund, that this is not a case of mere "convergence," but that the true torrenticolous fauna has found another refuge here.

The common fishes of this region are *Cottus gobio*, and sometimes *Lota vulgaris*; in trout-pools in our country the trout and minnows spawn here, close to shore.

β. The Sandy-Beach Community

This is again a lotic company, whose home is by the shifting margins where the scouring action of sand particles reduces plant-growth and certainly does not encourage the development of a rich fauna. Except for rocky shores, which are nearly barren, this is the poorest region of a lake: *Gammarus pulex* is the species most constant in occurrence; some Oligochætes, as *Naïs elingius*, burrow in the sand. Nematodes may be fairly plentiful, and water-mites, especially species of *Lebertia*, follow these hosts; for the rest, the fauna is mainly a reduction-version of type α, without the large-bodied animals. Wesenberg-Lund particularly notes the frequency of *Molanna*, a caddis which makes a flat, tortoise-like case of sand grains.

In both these regions, littoral Cladocera (as *Sida crystallina*, with its glandular dorsal adhesive organ) and *Canthocamptus* are found, rather sparsely, and *Fredericella* and *Plumatella* form branching colonies upon the stones.

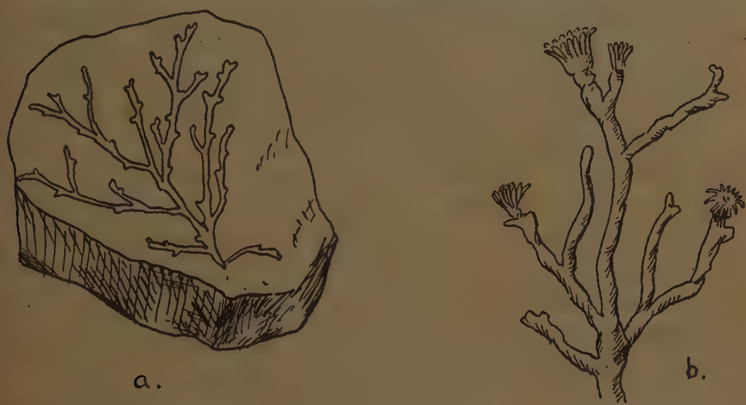

FIG. 72.—*a*, *Plumatella repens*, creeping form on a stone from wave-washed littoral; *b*, *Fredericella sultana* (after Kraepelin, much enlarged): erect type found in still water.

Below the limit of wave-action, plant-zoning follows as for the later series of Phase II.

PHASE II.—*Quiet Littoral*

On gently sloping shores, the littoral vegetation flourishes, and soft mud accumulates about its roots. The flora shows marked zonary distribution, grading from land-types through a marshy zone of emergent vegetation (*Scirpus*, *Carex*, *Phragmites* . . .) into a second belt of rooted plants with floating leaves (*Potamogeton*, *Nuphar*, and *Nymphæa*). Below this comes a submerged vegetation-belt of *Myriophyllum*, *Elodea*, *Chara*, and *Nitella*: the last-named usually extends to the outward limit of the true littoral zone. This is the general type for temperate lakes, subject to modifications, as we shall see. In lakes of Arctic type and stony littoral, few plants are found but Algæ, and Diatoms predominate; in Baikal the three zones are dominated by *Ulothrix*, Diatoms, and *Draparnaldia*, in descending order.[9]

IIA. *Zone of Emergent Vegetation*

The *Scirpus-Phragmites*, or "reed-swamp" zone, is really of the marsh-type rather than truly lacustrine. Other plants found here are *Iris*, *Sparganium*, *Menyanthes*, *Hippuris*, with some few filamentous Algæ, as *Vaucheria*, also frequently *Botrydium*, and quite a wealth of smaller Protophyta, especially Desmids, in a green slimy coating about the shoots of the emergent plants. *Hydra* and Nematodes and small Oligochætes are the most abundant members of the fauna, with small Hydrophilid and Dytiscid beetles (*Hydroporus palustris*, *Hydræna* species, and *Donacia* on the *Sparganium*), littoral species of Cladocera, larvæ of dragon-flies and midges, the water-spider, *Argyroneta*, and such caddis-larvæ as make cases of plant-material, especially *Limnophilus flavicornis* and *L. rhombicus*. The shallow margin is unsuitable to fishes, and even where the water deepens, conditions due to the felting Algal growth and copious presence of decaying matter exclude all but smaller Cyprinidæ.

IIB. *The Zone of Floating-leaved Vegetation*

Mud is the dominant feature of this zone: mud gathers at the roots of the pond-weeds and water-lilies, and mud-loving types of every group attain to rich development within the girdle. The little bladderwort (*Utricularia*) floats at the surface, the eel-grass (*Vallisneria*) sometimes thrusts up its ribbony leaves, and filamentous Algæ form a tangle upon the mud below. The mud-loving animals are collected from many varied groups, and there is scarcely need to mention any of them individually (see Chapter II). The groups most feebly represented are, of course, Ephemerids and Plecoptera, so many of whose nymphs are stone-clingers, and the Cladocera of limnetic habit. Most characteristic of the zone is the commencement of the strong development of Molluscan species. *Valvata* and *Limnæa* are the most common of the Gastropods, and reach their maximum development here;

PLATE X

(*a*) Little loch near Loch Ness, entirely surrounded and covered with vegetation: *Potamogeton natans*, *Polygonum amphibium*, *Menyanthes trifoliata* and others on the water. (From West's "Flora of Scottish Lakes.")

(*b*) A Welsh highland-pool, with its scanty zone of emergent vegetation followed by a well-developed *Potamogeton* zone.

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Sphærium and *Pisidium* attain great numbers. *Tubifex* species, many Dipteran larvæ, and leeches of the Rhynchobdellid type, with Nematodes, Ostracods, and Rhizopod Protozoa, are found in millions in the mud.

IIc. *The Zone of Characeæ and Myriophyllum* (*Submerged Vegetation*)

Characeæ flourish best in peaceful waters of high lime-content: both *Chara* and *Nitella* coat their shoots with incrustations of calcareous matter, and a rich limy slime accumulates about their roots. In this, the lowest littoral belt, the temperatures are very nearly even through the year, and the growth of plants almost unchecked, so that there is no lack of food or oxygen. This is the richest of all the lake-zones, and to it many of the littoral types resort for winter shelter, while *Coregonus* species, the deep-water lake-trout, come to its edge to spawn. (Cyprinids usually spawn above, in the summer growth of plants with floating leaves.) The fauna is much like that of the zone above, with the exception of a rich development of littoral species of Cladocera and Copepoda, and a loss of some of the confirmed burrowing-types, for whom the limy mud is not quite suitable. Among Mollusca, *Sphærium* falls off considerably in numbers: *Pisidium*, *Valvata*, and *Limnæa* are still quite common.

In Scandinavian and in Scottish lakes, with humus-impregnated waters and steep shores, the littoral zone has a peculiar character; the vegetation is much poorer as a whole, and in the narrow "emergent-zone" *Phragmites* and its usual congeners are largely replaced by *Equisetum* (horsetail) and *Menyanthes* (buckbean). The *Potamogeton* girdle is sometimes better developed, but below it comes a zone of *Littorella*, *Ioëstes lacustris* (Quillwort), and of Bryophytes.[10, 11, 12, 6] The littoral fauna in such lakes shows great reduction, probably in consequence of the scarcity of lime. Some of the plateau-pools in the Welsh area have this general facies.

B. The Sub-Littoral Zone

Here temperatures vary little through the years and the water is very still in general; the light is extremely feeble, and the scanty plant-growth mainly consists of "felting" of Algæ—especially *Oscillatoria*—and of Diatoms, which may be very numerous. Steady and slow accumulation of bottom-sediment takes place, and, of all the animal-life—which grows more and more scanty as the depth increases—the most important are Lamellibranchs and Chironomid larvæ. These forms, for whom the mud is shelter and the detritus derived from higher zones sufficient nourishment, may reach a very great development here. In some North German lakes the empty shells of *Unionidæ*, mixed with accumulating sediment, form vast banks of deposit at the outer fringe of the sub-littoral zone.[13] In its upper portion, *Unio*, *Anodonta*, *Dreissensia*, *Valvata*, and *Pisidium* live in great numbers, but towards its lower boundary all these except *Pisidium* disappear, and with them the littoral Crustacea, larvæ of Trichoptera and Ephemerids, and most Oligochætes.

In lakes of the Scandinavian type, mentioned above, the accumulation of bottom-deposits here is very slow; little material settles to the floor but fragments of plant stems and leaves, a few shells of littoral molluscs, and just a little very fine-grained mud. The fauna is extremely sparse, and all Mollusca but *Pisidium* may be absent from the sub-littoral zone. *Pisidium pusillum*, in Scottish lochs, is found as deep as 750 feet: it is a species very often found in humus-laden waters.

In general, the life of the sub-littoral zone is governed by the rapid disappearance of rooted vegetation at its upper limit and the slow extinction of mud-felting types towards its lower—consequent on lack of illumination. This series, together with the thickness of the overlying water-stratum, conditions general poverty of oxygen and "home-grown" food, on which depends the diminution of the fauna. In a rich lake, on calcareous substratum, bivalve Mollusca, feeding

on detritus, and very sluggish in their habits, with low oxygen-requirement, may reach a great development in the upper portion of this zone, but all except the very smallest types disappear suddenly above its lower limit. In "humus-lakes," the bottom fauna is poor, especially in Mollusca; *Pisidium* takes the place of larger bivalves here.

C. The Deep-Water Region

Below the vegetation-zones goes on a slow, steady deposition of sediment drifted down from littoral and pelagic regions. The temperature varies little from 4° C.; there is no light, and for long periods the deep water is cut off from gaseous interchange with the atmosphere. Conditions are unfavourable for most animals; the only food-supply comes from the "organic rain" of particles falling from above, and the richer this supply the poorer the conditions from another aspect, since the slow decay of such organic matter gives rise to noxious putrefaction-products and robs the water of its oxygen. As a general rule, animal life decreases as the depth increases: the fauna of the bottom comprises altogether not many species, and its constitution varies according to the type of lake.

In lakes with gently-sloping shores and a wide belt of littoral vegetation, where food-supply in upper layers is high and plankton rich, masses of detritus, rich in organic matter, accumulate to form bottom-deposits of a type known as "Faulschlamm," or "Gyttja."[14] In these "*eutrophic lakes*," which are particularly characteristic of the Baltic area, the bottom fauna is poor in species, and at profound depths only those survive which can endure oxygen-scarcity and feed on detritus, but those whose physiology is adapted to such conditions may reach enormous numbers, as food—of a sort—is plentiful for them. In a sense, the greater their numbers the better the conditions for them all, since by consuming the food-material they save it from putrefaction, and most of such feeders are insect-larvæ, so that their own decay takes place elsewhere. *Chironomus* larvæ of the

plumosus type make up the bulk of the bottom-population here; next to them in importance are *Tubifex tubifex* and *T. hammoniensis*.[15] We notice in both types the presence of dissolved hæmoglobin, giving a red colour to the blood, a point to be returned to later, in discussion of the fauna of sewage-polluted waters (Chapter X). Other species are few: the most important are Nematodes, *Pisidium spp.*, and larvæ of *Corethra plumicornis*.

In lakes with steep and rocky shores, with scanty littoral zones, as in sub-Alpine regions, the water is clear, and bottom sediments consist mostly of mineral matter, with little organic substance to decay. The oxygen-content of the deep waters is therefore well maintained, especially since under the transparent water the "feutre organique" (Forel) of green Algæ can extend to quite great depths. The food-supply in profound regions of these "*oligotrophic lakes*" is far less in quantity than in the eutrophic, and this scarcity governs the development of a fauna which, though poor in individual numbers, is richer in species than in Baltic lakes, owing to the better oxygen supply. A number of littoral and sublittoral species are sparsely represented here (see pp. 185, 186). These have been called the "*Tanytarsus lakes*" by Thienemann,[15, 12] as the dominant species of Chironomidæ are members of the *Tanytarsus* group: a typical form is *Lauterbornia coracina*. *Tubifex velutinus* and other microphages may attain considerable numbers.

Lakes of a third type, called "*dystrophic*," are the "*humus lakes*," studied especially in Scandinavia, whose peculiar littoral zoning we have already mentioned. Their waters, brown with humic acids, are practically clear of floating life, but plant-material from the littoral and from the outer world makes up most of the bottom-deposit, which is coarse in grain and decomposes only very slowly, owing to the peculiar properties of the water. This deposit has been called "Torfschlamm," or "Dy." In the deep-water region, as well as poverty of food-supply, there is also very serious oxygen-scarcity; even at slight depths the dissolved oxygen is often almost *nil*, perhaps because of the very frequent

presence of iron in the water. The zooplankton live pretty well on detritus, but phytoplankton suffers from the scarcity of food-material in solution, decay being retarded. Life in the profound regions of such lakes is at a minimum; in Scottish lochs of this type a few Rhizopoda and Cyprids, *Pisidium pusillum*, *Chironomus* larvæ, with a few Oligochætes and Nematodes, never in any mass-development, make up the total.[16]

Although the clear sub-Alpine lakes receive the palm for *variety* of bottom-species, the eutrophic lakes support the richest population, numerically speaking. *Chironomus* larvæ in their depths attain to vast numbers and are food for many fishes—perch, roach, carp, bream, and all Cyprinid species feed on them.

Even the depths of certain lakes in which the oxygen-content of the lower strata remains at *nil* for several months in summer are not devoid of life. In Lake Mendota, in waters devoid of oxygen for so long as three months at a time, there is an Invertebrate fauna of bottom-living Protozoa, *Chætonotus*, *Candona*, *Corneocyclas* (a small Lamellibranch), red *Chironomus* larvæ, and a few *Tubifex*. Some of these creatures seem to pass into a resting-phase in which metabolism is suspended, during the anaërobic period; but not all become inactive, and Juday suggests [46] that some of them may derive their oxygen from splitting-up stored glycogen, as do some parasites. One wanderer into these depths, the *Corethra* larva, rises at night to surface-waters, better aërated, and probably lives through the day upon the store of oxygen which has diffused into its air-sacs. Many of the animals of abyssal depths in Lake Leman have manganese within their tissues, and it is conjectured that this may serve them as a catalyst, facilitating absorption of oxygen at low tensions, although its presence is not limited to the deep-water fauna.[47, 48]

A second aspect of the study of life in the deep-water region is that which chiefly concerned its pioneer, Forel: the problem of the possible existence of a fauna limited to these great depths and specially adapted for a life under such conditions. The fauna of the ocean depths includes a number

of such "bathophilous" types, distinguished by transparency of body or the development of strong red and black pigments, and by prevailing blindness or else hypertrophy or anomalous structure of the eyes—features which are referred to the weak light, or darkness, at great depths. No lake has depths at all to be compared with those of the great oceans, but Forel argued, from a series of comparisons,[1b] that the development of abyssal fauna in the ocean was conditioned mainly by the absence of light and of vegetation, and that we might expect to find a parallel to it in lakes below the zone of illumination. He found in lakes of the sub-Alpine regions certain peculiar types, many of them common to the deep-water zone of a number of the lakes, and classed at first as separate "profound-species" of their genera. Two blind Crustacea—*Asellus Foreli* (so-called at first: later assimilated into the species *A. cavaticus*) and *Niphargus puteanus*—were important members of the assemblage, which also included some small, thin-shelled *Pisidia*, classed at first, by Clessin, into nineteen new species, a *Limnæa* (*L. abyssicola*), a form of the Polyzoan *Fredericella*, considered to be new, because it had small colonies, standing freely on the mud, instead of the usual creeping branches, a *Hydra rubra*—all these in quite large numbers. A blind *Gyrator cæcus*, a *Dendrocœlum* with eyes greatly reduced, and a few Turbellarians, e.g. *Plagiostoma Lemani*, colourless and very transparent, though not blind—these forms, less general in these waters, as well as several Foraminifera, were considered none the less as "deep-water species."

Forel considered that the bulk of these were new species derived from types originally littoral, along certain lines of adaptation, of which the chief were:

(*a*) Reduction of pigment } related to the poverty of light.
(*b*) Reduction and loss of eyes }

(*c*) Reduction of shells in Mollusca, related to the stillness of the water and scarcity of food.

(*d*) Loss of fixed attachment, as in *Fredericella* colonies, and in the egg-masses of Mollusca, here laid freely on the bottom—related to the stillness of the water.

The two blind Crustacea he classed apart as migrants from the subterranean waters into the lakes. Forel's conclusions have been in the main confirmed by later workers. It is true that many of the separate species—notably of *Pisidium*—now rank as mere varieties, or habit-forms, but this re-grouping only serves to strengthen the chief of his conclusions, that the deep-water fauna (with the exceptions named) consists of migrants from the littoral region which have to some extent become modified by the conditions they encounter.

One of Forel's beliefs, that the great pressure of water at these depths may influence the physiology of certain types, especially of Dipteran larvæ, must be abandoned. Early workers were perplexed to understand how these larvæ could complete their metamorphosis, and a theory of "neoteny," or "pædogenesis" (*i.e.* sexual reproduction during the larval phase), was advanced to meet the case; but this received its death-blow from the observations made by Fehlmann [17] on *Pelopia* larvæ living at a depth of 80 metres in Lake Lugano. Egg-laying at the surface, the slow sinking of the eggs, development and moulting of the larvæ, and, finally, the rise from bottom to surface for metamorphosis—all were ascertained with certainty, and any strong influence of water-pressure discredited by the fact that all the larval-phases could ensue with equal regularity at the bottom or in the shallow tanks of a laboratory.

More recent work has shown the importance of the character of bottom-deposits in determining the range of "eurybathic" species (*i.e.* those which can extend a long way vertically).[18, 19, 20]

Another question concerning the origin of some deep-lake dwellers has been raised already, in Chapter V. Outstanding cases of stenothermous Ice-Age relicts in deep waters are, from Forel's own group of sub-Alpine lakes, the two blind Crustacea (also found in waters of subterranean origin) and some other forms which occur elsewhere in the cold littoral zone of higher or more northern lakes, or in springs—as a number of Hydrachnidæ (e.g. *Lebertia tau-insignata*), Ostracoda (Cytheridæ), and Penard's Rhizopods, already mentioned in

preceding chapters. Peculiar to the depths of northern lakes are the "glacial-marine relicts," *Pontoporeia*, etc.

Ekman has argued [21] that in European lakes there can be no deep-water fauna *sensu strictu*, since none of them attain sufficient depth for complete extinction of sub-littoral species, nor has sufficient time elapsed since the Ice Age, which seriously affected their formation and their fauna, for the evolution of endemic species within their depths, such as they are. It is true that, in the few extra-European lakes of archaic origin and very considerable depth which have been studied —notably Baikal and Tanganyika—the fauna below the 600-metre line has a peculiar character, and some species remind the biologist of abyssal oceanic types more strongly than do any in European lakes. In Baikal, whose greatest depth is believed to be about 1700 metres, this abyssal character is taken on by species whose range has its highest limit below 600 metres, and a high percentage of such species are endemic. In the case of Amphipods, the endemic species include a good half of the total number recorded from all fresh waters of the globe; below 200 metres they begin to develop transparency and loss of pigment, and these features become more noticeable as we trace them downwards: some abyssal Gammarids have bodies as transparent as crystal. Side by side with this feature goes degeneration of the eyes, and compensating development of tactile hairs, with lengthening of antennæ, claws, and all limbs, in proportion to the body-size. Below 600 metres all are blind, and some are of gigantic size (see Chapter V, p. 131, and [9]). Some of the fishes of abyssal depths are scaleless and transparent, with great, goggling eyes, and skeletons so poor in lime that in the hand they feel as light as paper. How far such characters are to be referred to abyssal conditions, and how far to special chemistry of the water (which is very poor in lime), or to the prevalent low temperature (which naturally leads to gigantism, by deferring sexual maturity), or to the isolation of the lake (a weighty factor in the origin of endemic species)—these are matters difficult to determine. Certainly, some of the tendencies so marked in this abyssal fauna are evinced in less

degree by some inhabitants of the greatest depths of European lakes.

Pelagic Region of the Free Waters in Lakes

Besides the variable factor of light-penetration (discussed in Chapter III) the most important of conditions which affect pelagic life are temperature and oxygenation. The surface-temperatures are affected by atmospheric contact and also by insolation direct. As water attains its maximum density at 37°F about 4° C., it follows that, in a deep, stagnant lake, there would be established in the summer a regular thermal stratification, with higher temperatures at the surface grading down

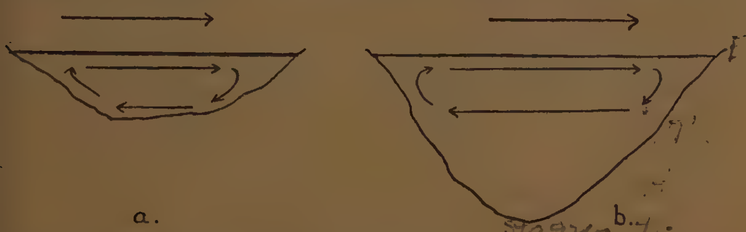

FIG. 73.—Wind circulation. *a*, Complete circulation in a shallow lake; *b*, partial circulation in a deep lake.

to a minimum at this temperature. But even if we neglect the influence of rivers flowing into and out of the lake, its surface-waters are very seldom stagnant. Wind-action drives them in a direction constant for the time being, and the tendency to pile up against the leeward shore is compensated by a deeper current running in counter direction. "Wind-circulation" in a shallow lake may be complete, equalising temperatures and dissolved gas-content throughout the mass. In deeper lakes, only the upper mass, or "epilimnion," is affected, while the lower body, or "hypolimnion," remains stagnant for long periods, with constant temperature of 4° C., and gas-content unaltered through atmospheric influence, but dependent on biological processes occurring within the deep-water region (see Figs. 73, 74). Between these layers comes the "metalimnion," or "thermocline" (Fr. *couche de saut*

thermique, Ger. *Sprungschicht*), where temperature alters rapidly within a narrow vertical range.

Forel distinguished three main types of deep lakes :

1. *Warm lakes*, like those of Italy and sheltered Alpine slopes. In these the surface-temperature never falls below 4° C., and is usually higher, so that thermal stratification remains direct, the temperature falling with increasing depth.

2. *Cold lakes*, as in high plateaux and polar regions. The

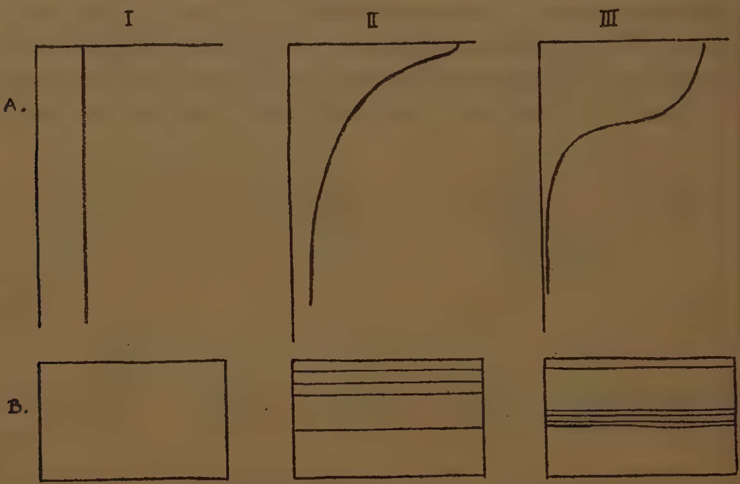

FIG. 74.—The temperature-cycle in a deep lake (after Wedderburn). A, Graphs of temperatures and depth ; B, isotherms. Phases : I. December–April, temperature practically uniform ; II. May–July, temperature falling from top to bottom, gradient steepest near the surface ; III. Aug.–Nov., establishment of a thermocline.

39 °F.

surface-temperature is never higher than 4° C., and thermal stratification is thus inverse.

3. *Temperate lakes*, as over most of Europe. The surface-temperature is higher than 4° C. in summer, lower in winter ; thermal stratification is reversed at the change of seasons.

In lakes of this third type, which principally concern us, two periods of stagnation of the hypolimnion—winter and summer—are separated by a spring and autumn period of upheaval and temporary full circulation. In the winter stagnation-period, direct thermal stratification leads from

4° C. at the bottom to freezing-point at the surface, without any marked thermocline. In spring the surface-waters warm, increasing in density as they pass from 0° to 4° C., so that at first they sink towards the bottom, and set the whole mass into a temporary full circulation. As warming proceeds, the thermocline begins to form, at first in fairly shallow water, and sinks lower, often reaching a depth of 20 or 30 metres in temperate lakes by autumn. The autumn cooling of the surface-waters causes a fresh establishment of convection-currents, resulting in the autumn period of full circulation,

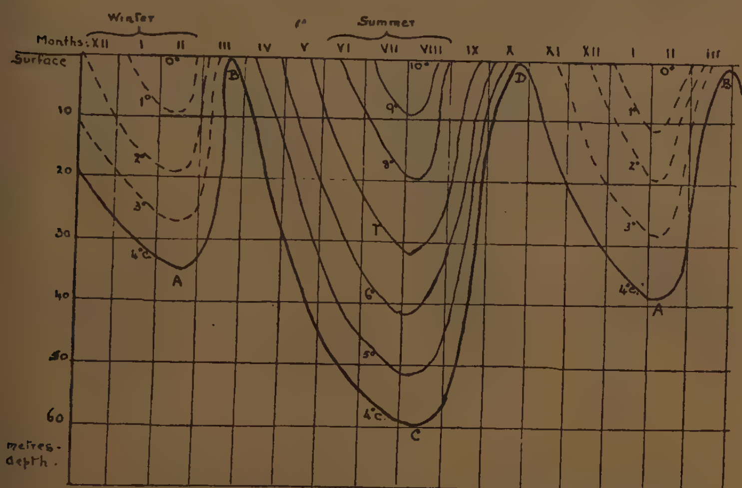

FIG. 75.—Seasonal changes of temperature in a deep lake (after Forel).

after which winter-stagnation once again sets in. This is a very broad description of the general relations: infinite variations are found in different lakes, but for our purpose it must serve to show the very great importance of the spring and autumn periods of upheaval, when full circulation mingles epi- and hypo-limnial waters, and tends to equalise their solution-content, and also the distribution of suspended matter.

Communities of the Free Water

The Nekton.—Most of the Cyprinidæ, discussed in the preceding chapter, are equally common in lake waters, where they haunt the littoral zone, especially in summer. The pike, which feeds on other fishes, is more often found in lakes than in slow rivers. The lake Salmonidæ (*Coregonus* species), whitefish, pollan, and powan are usually pelagic in deep waters, but come at least to the sub-littoral zone to spawn. The importance of the benthic fauna for the feeding of

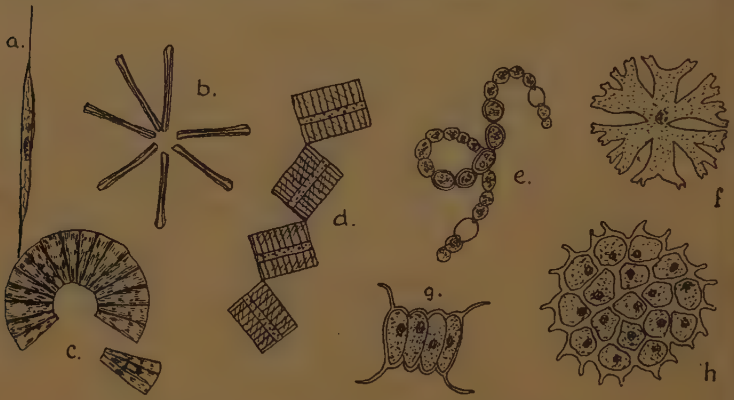

Fig. 76.—Some plankton-Algæ.

a, Rhizosolenia, *b, Asterionella*, *c, Meridion*, *d, Tabellaria* — Diatomaceæ.
e, Nostoc, Cyanophyceæ.
f, Micrasterium, Desmidaceæ.
g, Scenedesmus, *h, Pediastrum* — Chlorococcaceæ.

Cyprinidæ has already been mentioned; no less important, for the young of all lake-fishes, and for the adults of some species, is the next community which we must discuss.

The Plankton.—The general characteristics and mode of maintenance of this important lake-community have been shortly discussed in Chapter II. For the most part, we must refrain from special consideration of the phytoplankton, which is recruited from a number of groups. Perhaps the most important of these are Cyanophyceæ, or Blue-Green Algæ (as *Chroococcus*, *Anabæna*, *Oscillatoria*), Diatomaceæ (as *Melosira*,

Fragilaria, *Asterionella*), Dinoflagellata (as *Ceratium*, *Glenodinium*, *Peridinium*). Chlorophyceæ and especially Desmids reach as a rule their best development in shallow lakes or ponds. Bacteria may be numerous in the plankton.

The problem of how to remain afloat, for bodies slightly heavier than water, is serious, and in those plankton-plants which have no active swimming powers we find a great variety of devices which tend to retard sinking. Some have inclusions of gas-vacuoles or oil-drops, which reduce the average weight of the whole mass; the appearance of "water-bloom"—which may be formed by various Algæ, especially *Anabæna flos-aquæ*—is due to rapid multiplication of plants which float close to the surface, buoyed up in this way. Other devices found in various members of the phytoplankton contribute to the extension of floating-surface, by elongation of the main axis of growth (as in *Synedra* and *Rhizosolenia*), development of fringing hairs (as in *Chætoceras*), production of gallerta-masses to enclose colonies (as in *Pandorina*) or single cells (as in *Sphærocystis*), and aggregation of unit-bodies into long chains (as *Tabellaria* and *Fragilaria*).[22]

FIG. 77.—*Notholca longispina*, a plankton - Rotifer (after Steuer).

Some species among the zooplankton have quite a considerable development of spines or other extensions of the body-surface, but these are best developed in the few powerfully-swimming predaceous Cladocera (see Chapter II), where the long axis of the body is prolonged into a rudder-like organ, notably in *Bythotrephes*. Production of gallerta is very rare: only *Holopedium gibberum* and one or two Rotifers have such an including sphere. Many plankton-Crustacea hold in their tissues large included oil-drops, derived from the phytoplankton on which they feed; undoubtedly these help to buoy them up, but, on the whole, reduction of body-size (with

its corollary, increase of surface) and absence of heavy coverings or skeletons, are sufficient in themselves to enable these animals—all of which are active swimmers—to maintain their level in the water, although, when dead, their bodies very slowly sink to the bottom.

In some of the temperate European lakes, a phenomenon known as "seasonal polymorphism" is very marked among the plankton-types. A series of variations during the summer season of rapid multiplication may lead to the temporary predominance of what in many cases have been classed as

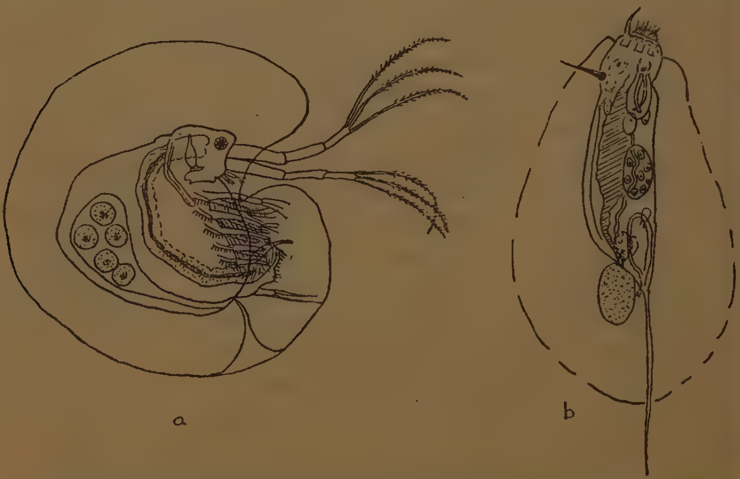

FIG. 78.—Two plankton animals with gelatinous floats. *a*, *Holopedium gibberum* (Cladocera): diameter about 5 mm.; *b*, *Mastigocerca setifera* (Rotifera): diameter about 0·5 mm. (after Hesse).

local races or sub-species, while the restitution of the original type takes place towards the winter. Wesenberg-Lund, studying these variations in Danish lakes, found that in species so widely separated in classification as those of e.g. *Ceratium*, *Asplanchna*, and *Bosmina*, there was a general manifestation of summer varieties with well-marked crests, long spines, or other extensions of the general surface, and to the production of more compact forms in winter. He formed the theory that these variations were closely

related to the seasonal changes in temperature of the water, as determining density and viscosity. Reduced viscosity in summer would increase the difficulty of floating in the water, and these "summer forms" seemed well adapted to compensate this difficulty.[23, 6] A number of other workers have more recently investigated seasonal polymorphism in various plankton-species, and their results do not in general confirm

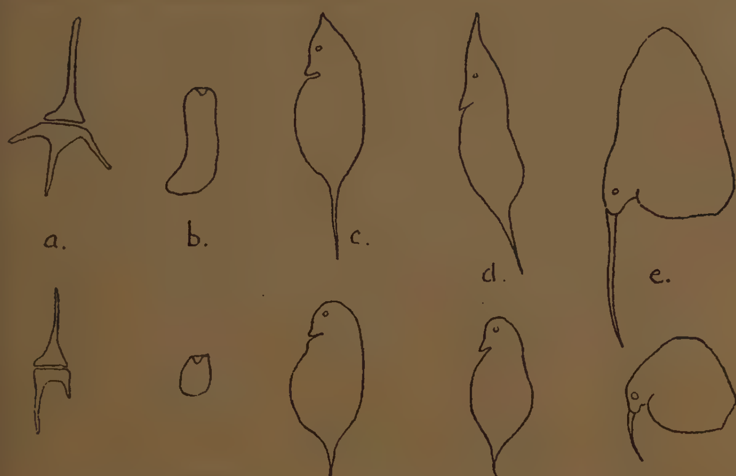

FIG. 79.—Seasonal variation in some plankton types (after Wesenberg-Lund). *a*, *Ceratium hirundinella*; *b*, *Asplanchna priodonta*; *c*, *Daphnia hyalina*; *d*, *Hyalodaphnia cucullata*; *e*, *Bosmina coregoni*. Upper row: summer forms. Lower row: winter forms from the same lake.

the theory. We need mention only two special cases—that of the highly irregular series of variations in *Ceratium hirundinella* in different localities ([24] and references therein), and that of *Anuræa cochlearis*, beautifully elucidated by Lauterborn,[25] in which the summer forms are those with reduced development of spines. The type of seasonal polymorphism studied by Wesenberg-Lund seems to be limited to shallow lakes with a wide annual range of temperature, as we might expect to be the case, if his explanation be correct.

VERTICAL DISTRIBUTION OF THE PLANKTON

The plankton is not evenly distributed throughout the whole body of water in a lake; as a rule the surface-metre is not thickly populated, and the main mass is found from about 1 to 30 metres. Often the plankton thins out rapidly below this, but in some cases it may be plentiful even below 100 metres.[26] There is a marked biological stratification of the plankton; the phytoplankton naturally characterises the upper layers, where light penetration is good, and the green Flagellates, which as a rule are positively phototropic, come very near the surface, as do Cyanophyceæ, Desmids, and free filamentous Chlorophyceæ. Diatoms and Peridinians are often found in greatest numbers at about 10 feet below the surface. It has been suggested that a low light intensity may be the optimum for forms with yellow-brown chromatophores. Each species of the phytoplankton, at its season of maximum development (see later, p. 203), tends to come nearer to the surface and crowd out the other types. In lakes of very clear water the surface-layers are often thinly populated.[27]

Among the zooplankton the vertical disposition is very complicated. As a rule, Rotifera are characteristic of the surface-layers, while in Crustacea the young are generally to be found fairly near the surface, their elders at lower levels. Each species has its characteristic range for every type of lake, and the analysis of all the factors which determine it is a complicated matter. Certainly temperature is in some cases an important factor; cold-water stenotherms such as *Limnocalanus macrurus*, in temperate lakes, keep to the deeper levels, for example.[28] A factor more generally operative is that of light: Crustacea of the plankton are often negatively phototropic to strong light in their adult phases, while their young may give the reverse reaction. Ruttner has shown that, in a frozen lake, the mere removal of the covering of snow, admitting light, may cause profound changes in the stratification of the zooplankton.[29] Possibly the preference of the young Crustacea for soft algal foods may have something to

do with their maintenance in upper strata; while Birge has demonstrated [30] that less effort is required to keep them there than for their elders: the sinking-rate of adult *Daphnia*, when motionless, is three or four times that of the newly-hatched young. The question of vertical distribution is complicated by the very marked diurnal vertical wanderings of most Crustacean-planktonts. It is the general experience of workers that plankton-catches at the surface taken during the night contain far greater numbers of animals than surface-hauls made by daylight. In daytime the fullest catches are made at depths which vary according to conditions and species. Vertical migrations are the regular habit of very many species, some of which have a great migratory range. In Lake Neuchâtel [31] the average diurnal range of *Daphnia hyalina* is 55 to 80 metres, that of *Diaptomus laciniatus* between 60 and 80 metres; but young *Cyclops*, *Nauplius* larvæ, and the common Rotifers have scarcely any trace of vertical migration of this kind. Several factors may be supposed likely to govern these diurnal migrations—the chief are temperature and light. Stress is thrown on the latter, especially in view of Ruttner's observations—already quoted—under the ice, which show that under these conditions, when temperature is even and the water held in stillness, the migrations do take place if the snow-covering be removed to admit the light. But in spite of this important work, the question is not yet finally settled, as there seems to be discrepancy between results obtained in different localities.[32] Further observations on this interesting topic are needed.

Horizontal Distribution of the Plankton

The question whether the plankton is evenly distributed in relation to the surface-dimensions of a lake, or whether aggregations occur in particular places, is of some importance in relation to lake-fisheries, as determining the feeding-grounds of the fishes. Most observers agree that distribution is fairly even over the free central portion of the lake, though there are some records of unusual aggregations, or "swarms,"

generally composed of members of one, or at most two, Crustacean species.[30, 31, 32, 33, 34, 35] Such local concentrations may perhaps be caused by drifting, due to wind or currents, as certainly they are formed in the ocean at the margins of influence of currents; they may be formed by active wandering of the species into some attractive spot, or they may arise by rapid multiplication in places where conditions are peculiarly favourable. Most students of the question do not think such aggregations sufficiently common to be of much importance, but in Lough Derg they seem to be peculiarly frequent in the littoral region, in summer, and to be formed by several species, probably through drifting due to wind.

Plankton is richest as a rule in lakes with a broad, gently-

FIG. 80.—Vertical migration and "Uferflucht" of the plankton (after Burckhardt). A, Downward migration in daytime; B, vertical upward migration at night, leaving shore-zone clear of plankton.

sloping littoral, and in the shallow bays within such lakes [33, 36]; but in the actual littoral zone the true limnetic species are generally scantily represented, especially in depths of less than 10 metres. The concentration of the limnetic plankton towards the centre—known as the "Uferflucht"—has been explained by Burckhardt [37] as an effect of the diurnal vertical migration: animals floating in the littoral zone, migrating downwards in the daytime, must turn along the shore towards the lake-centre to reach the limit of their vertical range; the upward night-migration would be purely vertical, not tending to bring them back towards the shore (see Fig. 80). The suggestion is interesting, and this view might perhaps be extended to cover the wider question of the origin of limnetic from littoral species; it is true that many of the plankton-types are found nearer to shore in their young stages.

Periodicity of the Plankton

The volume and constitution of lake-plankton vary according to the seasons. In temperate lakes the total plankton always attains its maximum development in spring or early summer. After this comes a gradual falling-off, followed by a rise to a second, smaller, autumnal maximum, preceding a more rapid fall to a winter minimum during the first two months of the year. The composition is changing in proportions the whole time: each plankton-species, animal or plant, has its own special season (or two seasons, in some cases) of maximum development, and different species dominate the general aspect by turns. The approximate coincidence of the maxima of a number of species in spring and autumn determines the general vernal and autumnal maxima. What are the factors determining the incidence of maxima?

In the zooplankton, the organic rhythm of reproduction in each species is naturally very important. Most species have a period of rest, or of extinction of all active members, leaving only the resting-eggs during the winter, and one of rapid multiplication in the spring, when temperatures are higher, and food abundant. Some species, e.g. *Leptodora kindti*, *Bythotrephes longimanus*, have only a single maximum in early summer; others have a second, roughly coinciding with the autumn general maximum. This second, though it may be largely determined by the internal rhythm, is certainly correlated, at least in time, with the abundance of plant-food available (see Fig. 31, p. 59).

The case of the phytoplankton species is rather more difficult. Here, as in the zooplankton, each species has its characteristic period of maximum development. The succession of periods of dominance differs in detail in each separate lake, and every year may show some differences in proportionate development of species, but as a rule Diatoms are dominant from late autumn to early spring, *Ceratium hirundinella* in spring gives place to Cyanophyceæ and Peridinians, which, with Chlorophyceæ, are mostly summer forms.[38, 5, etc.]

The occurrence of the autumn general maximum is often largely due to increase among the Diatoms, and its cause has been much discussed. Direct influence of temperature cannot account for it: probably the question is one of supply of dissolved salts in the water. Many workers seek to correlate both vernal and autumnal maxima with the upheaval-periods at these seasons in lakes with a thermocline, when temporary full circulation brings up reserves of food-material from the hypolimnion.[39, 40] But we must not accept this most attractive theory as the sole explanation of the facts, since autumn maxima—as well as vernal—are known to occur in lakes which have no thermocline, as in Lough Derg.[32] Apparently in this lake they are related to the seasonal flooding of the River Shannon, which traverses the lake. Flooding releases and sweeps down large quantities of organic detritus, which may directly nourish the Crustacea, and also raise the nitrate and silicate content of the water, thus providing for an increase in phytoplankton. Conditions in this lake are very "special"; probably in every lake some local factors contribute to the very complex group affecting plankton-production; statistics from as many different localities as possible are therefore desirable.

The Lake as a Biocœnotic Entity

An outline of the biology of the several typical regions of a lake cannot fail to include some mention of the relations between these regions. It is a familiar conception that no living being is truly independent, but holds its life conditionally upon the harmonious working of its own scheme with that of other elements in the natural economy: very little effort of the mind is needed to enlarge the conception so as to include appreciation of the linkage of community with community. The lake, of all freshwater bodies, ranks most nearly as a world within itself, and in this cosmos each community reacts upon the others and in turn receives their influence, so that throughout the whole intricate web we trace one bold design: the life and evolution of the lake itself as a biocœnotic entity.

We have seen how the needs of respiration and nutrition run, like master-threads in the design, from phytoplankton through to fish-production; we must also know how little may disturb the balance of life within the mass. Too copious production of phytoplankton, such as sometimes occurs at the vernal outbreak of "water-bloom" in a eutrophic lake, may crowd the floating animal-life from access to the surface, form a matting in the water under which poisonous gases, augmented by the products of decay of this great mass, accumulate without diffusion to the surface, leading to the death of fishes and other animals; conversely, a scanty crop of phytoplankton fails to satisfy the demands of the fauna for organic food and oxygen, and so production is again impeded. But deeper considerations still than such as these must occupy us: in lakes the transformation of material has wider scope.

The inorganic salts brought down by rivers from the rocks and soil provide the food-supply of plants; some of these latter go to nourish animals direct, some, in decay, contribute to the organic rain of particles which falls upon the bottom of the lake, and in which portions of the dead bodies of the zooplankton are also included. This rain of material nourishes detritus-feeders, benthic animals of sluggish habit, such as Chironomid-larvæ and Mollusca, which by their own excretory function add a coprogenic element, rich in phosphates, to the slow accumulation of decaying organic sediment. The bacteria of putrefaction break down these substances to simpler forms (see Chapter IX, p. 244), from which bacterial action ultimately builds up nitrates and phosphates. These pass into the mass of water by diffusion, with the aid of vertical currents, and thus restore the balance—but this is not all. Insoluble matters, mineral sands and clays, brought in by rivers or derived *in situ* from coastal erosion by wind-raised waves, clouding the waters for a time, eventually sink to the quiet layers at the bottom and there accumulate to sediments. These, bulking larger than the scanty layer of coprogenic matter and the like, tend to obscure the organic layers and to shut them from access to oxygen-diffusion in the overlying stratum of water. The anaërobic putrefactive organisms can

work beneath the surface, but their action results in the production of substances of poisonous and malodorous character, ptomaines, hydrogen sulphide, methane, and so on, which are useless in such form for the nutrition of living beings. Hence those food-supplies which come into the lake from outside sources, after passing through a single cycle of organic life, must be impounded in its sediments and useless for the future, were it not for the intervention of another group of benthic organisms. The little Tubificidæ, the small

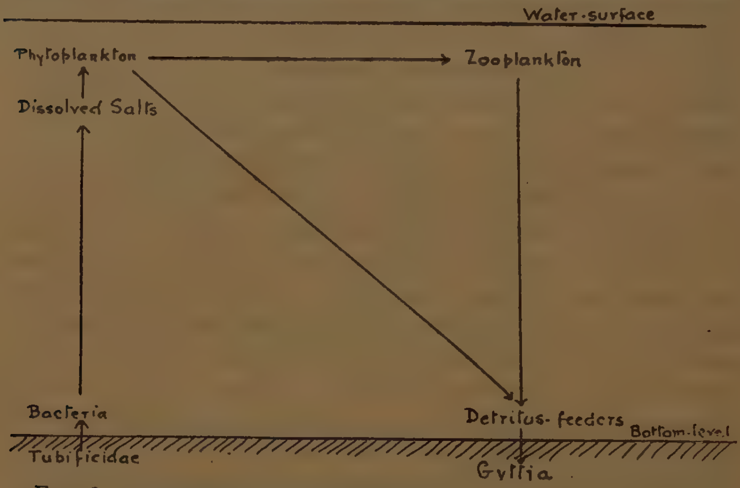

FIG. 81.—Circulation of food-material in a Eutrophic Lake (after Alsterberg).

red-blooded Oligochætes, which build their tubes like chimneys striking upward from the mud, are busily at work below the surface, after the fashion of their relatives the earthworms, the first ploughmen of the soil, although they do not move about like these and make aërating tunnels. Each *Tubifex* thrusts its body downward till the head is some 3 to 6 centimetres below the surface, passing beyond the coarser mineral sediment to attain the lower " nutritive-layer " of organic deposit.[38] The hinder end and tail project above into the water, and here the castings are voided, continually raising material from the anaërobic to the aërobic stratum, and exposing it to the full

cycle of bacterial action which converts it into available food-material once again.

The presence of abundant Tubificidæ depends upon two factors, food-supply and oxygen, for though, as we have seen, they can endure some scarcity of oxygen, they cannot dispense with it entirely. The region of their maximum development is usually below the epilimnion, in the zone of quiet sedimentation; but in eutrophic lakes with a high thermocline oxygen-scarcity below it reduces the *Tubifex* zone very considerably. In such lakes the slight development of these "sediment-transporters" abandons the organic deposits to drifting over by mineral sediments, and to an anaërobic decomposition which results in the production of "Faulschlamm," or stinking mud. The incursion of littoral vegetation, rather than drifting up by sediments, is fundamental to the passage of a lake of this type into, first, a shallowing pond, then a morass.

Oligotrophic lakes with steeply shelving shores, where the narrow band of littoral vegetation contributes little in the way of detritus, and phytoplankton production is limited by an induced scarcity of food, contain a deeper-going zone of Oligochætes, and gradually pass by slow accretion of bottom-sediments, mainly mineral in character, into the shallowing type of the eutrophic lake.

In lakes of humus-type, where iron in the water robs it of its oxygen, and holds up the action of bacteria, bottom-deposits are of yet another character. In place of the "autochthonous" (home-produced) sediments of the oligotrophic and eutrophic lakes, we have "allochthonous" material of drifted fragments from shore-living plants, preserved from total decay and accumulating in coarse-grained masses at the bottom, contributing nothing to the enrichment of the waters in solution-content. The phytoplankton is extremely scanty, owing to the starvation conditions in the water, but in the upper strata of the lake, where the water is fairly well oxygenated, the zooplankton may develop to moderate numbers, feeding upon the solid detritus from littoral plants. The bottom accumulations are peaty "Torfschlamm" (Dy), which piles up

rapidly, as there is little or no bacterial decomposition, and these lakes tend to fill in an astonishingly short time into stretches of moorland bog, invaded by advancing colonies of *Sphagnum*.

British Limnological Studies

We have no great lakes in Britain: by far the largest is Lough Neagh, in the north of Ireland, a shallow basin whose mean depth is only 40 feet, and its area, though very much above the average for all other British lakes, about 150 square miles. Our lakes are none the less of special interest, in relation to the geological history of our islands, sundered from the Continent at no very far-distant time.

The Scottish Highland lochs, in their narrow, rocky valleys, with barren, steeply-descending shores and peat-stained waters, strongly suggest in general aspect an affinity with the Scandinavian group of lakes in Europe. The Survey organised by Sir John Murray [39, 40] showed that the general biological features of this group—weak littoral belts, poor phytoplankton, and predominance of stenothermic species in zooplankton—are well-developed here: Arctic species common in the plankton are *Holopedium gibberum*, *Bosmina longirostris*, *Bythotrephes longimanus*, *Cyclops strenuus*, *Diaptomus laciniatus*, and *D. laticeps*; these are mixed, of course, with cosmopolitan types. A peculiar feature of the phytoplankton is the enormous frequency of Desmids: this is probably to be explained with reference to the peaty character of the water.[41] The "deep-water fauna" of the deeper lochs is very disappointing, and includes scarcely any of the characteristic forms of European deep waters, and none of the Baltic relict-species (see Chapter VI, pp. 126–127). Probably the character of the bottom-deposits, which are mostly of coarse plant-material, as in all humus-lakes, explains their scanty fauna.

In contradistinction to the Highland lochs, the lowland lakes of the Central Plain of Scotland were found by the Survey to belong distinctly to the Danish type of shallow lakes with well-developed littoral. The abundance of the phytoplankton in particular, and incoming of fresh species

into phyto- and zoo-plankton alike, together with the character of bottom and strong development of seasonal phases, all point to this affinity.[40]

The lakes of Cumberland and Westmorland have also received some study; some of them recall the Scottish Highland lochs in form and origin, others are greatly influenced by silting. This latter factor has been shown to be of great importance in determining the constitution of the phytoplankton.[42, 43] The Crustacean plankton seems to vary locally according to the depth of water in the individual lakes: it contains a well-marked Arctic element, and approximates to that of the Scottish and Scandinavian lakes in general type.[44]

The biological character of Lough Neagh is, as we might expect, more nearly akin to that of Danish lakes; the phytoplankton is very abundant, often colouring the water, and water-bloom a frequent phenomenon, as in these lakes, but one Arctic species—*Tabellaria fenestrata*—distinguishes it from the Danish type. The zooplankton is a mixed assemblage, with at least two species of northern affinities—*Bosmina longirostris* and *Mysis relicta*. This is an interesting example of a lake of mixed type.[45] The only other British lake whose biology has been carefully investigated is Lough Derg, already mentioned.[32] The lake is rather shallow, with a floor of marl upon a rocky bed; its biology, especially in respect of seasonal changes, seems to be dominated by the influence of the river which traverses it, making it a peculiarly interesting subject for study. So far as classification is concerned, it seems to stand nearest to Lough Neagh, as a "mixed type." Species of northern origin, as *Cyclops strenuus*, *Mysis relicta*, *Bosmina longirostris*, are mingled with a greater number common to lakes of the European plain. Desmids are scarce, but Diatoms and *Oscillatoria* are prominent among the phytoplankton.

This little summary will serve to show the interest attaching to lake-investigations in our small area, whose geology and general conditions are so varied that lakes of similar type may be separated by others of a totally different character. Much more research is needed. Ireland has a number of lakes too

large to be neglected, the little lakes of the Welsh highlands contain all the ingredients of a really pretty problem, and the meres of Cheshire, though of no great size, should afford fascinating comparisons with lakes of Danish type.

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CHAPTER IX

THE BIOLOGY OF SMALL AND PECULIAR WATER-BODIES

"Nor are the number, nor the various shapes of creatures, more strange, or more fit for contemplation, than their different natures, inclinations, and actions; concerning which I will beg your patient ear a little longer."—IZAAK WALTON.

Ponds

THE true distinction between lakes and ponds lies not in area, but in depth of water: a pond may be defined as a stagnant water-body in which the littoral zone of "floating-leaved vegetation"—pond-weed, water-lilies, water-crowfoot, and the like—extends to the centre, and its life greatly resembles that of the littoral zone of lakes, with some few special features.

One special character of many ponds, especially those on marly soil, is the great development of green Algæ. Near the shores float slimy masses of *Spirogyra*, *Mougeotia*, *Ulothrix* and other confervoids, buoyed up by oxygen-bubbles, products of their own carbon-assimilation processes; on all the stems of rooted plants are delicate green fringes of *Cladophora* and other branching filamentous types, while *Volvox*, *Pediastrum*, and *Hydrodictyon*, the water-net, and many Desmids float near the surface, and sometimes *Lemna* or *Salvinia* is mingled with them.

Littoral animals especially abundant in the ponds are Agrionid and Phryganid larvæ, Rhabdocœle Turbellarians, pond-leeches, newts and frogs, and air-breathing insect-larvæ, water-beetles, and pond-snails, that find a way to the surface over the abundant vegetation. The stillness of the water favours the presence of surface-skimming animals, and all the water-crickets, water-measurers, pond-skaters, as well

as swimming Hemiptera—water-boatmen and pond-scorpions—are at home in ponds. The bottom mud is largely occupied by *Sphærium* and mud-loving Dipteran larvæ, and Rhizopoda

FIG. 82.—Some typical members of the plankton of ponds (partly after Steuer). *a*, *Diaptomus vulgaris*; *b*, *Diaphonosoma brachyurum*; *c*, *Ceriodaphnia pulchella*; *d*, *Brachionus amphiceros*; *e*, *Peridinium tabulatum*; *f*, *Chydorus sphæricus* (not to scale).

move across its surface, the water-slater (*Asellus*) tiptoes so lightly that it almost seems to float, and *Gammarus* scuds sideways. The lily-pads harbour the interesting aquatic larvæ of a few Lepidoptera, and the few aquatic types of

Hymenoptera which parasitise pond-animals. The pond-mites are innumerable: indeed, in the crowded world of ponds space seems the only factor limiting the wealth of life, and parasitism, saprophitism, and epiphytism are much in evidence. We have already mentioned the growth of Algæ on the large plants; a parallel to this is found in the encrusting masses of Polyzoa and Vorticellids which attach themselves to shells of Molluscs, carapaces of Crustacea, and even to the opercula of fishes. Sticklebacks are the most common fishes in very small ponds; in large ones, Cyprinidæ, especially carp and tench, find easy living, and here the pike, feeding on these other fishes, may attain enormous size.

FIG. 83.—*Apus cancriformis*, dorsal view.

In ponds of recent origin, or those with harder bottoms, vegetation is far less rich; pond-weeds and lilies may be absent, and the best-developed plants *Chara*, *Myriophyllum* and the bulrushes. In such ponds the fauna also is diminished, and, as in the sub-littoral zone of lakes, pond-mussels (Unionidæ), which like bare bottom, are especially important. *Unio margaritifer*, the freshwater pearl-mussel, occurs in such clear ponds, and swimming beetles, Ostracods, and "scuds" (Amphipoda) are better developed than other usual types.

Ponds of sufficient extent have a true plankton, many of whose species are also to be found in the littoral zone of lakes, but some are sufficiently characteristic of ponds to constitute a plankton of distinct type, or "Heleoplankton."[1, 2, 3] Protococcaceæ, *Volvox*, and Desmids, Rotifers of the genus *Brachionus*, and, among Cladocera, species of *Simocephalus*, *Chydorus*, and *Ceriodaphnia*, with some *Diaptomus* and

Cyclops species, are very constant members of this plankton. Even in deep ponds, diurnal vertical migration is not well-marked.[4, 5]

A special class are the "impermanent ponds," subject to desiccation, and these include among their fauna especially Phyllopods—as *Apus* and *Branchipus*, polycyclic Cladocera; as *Moina*, Ostracods, and *Cyclops*: all forms which can survive drought-periods either encysted or as latent eggs (see Chapter IV).

The seasonal life of ponds affords many opportunities for interesting observations. On the whole, there is more maintenance of active life in winter than might be supposed: even under the ice one often sees actively swimming creatures.

FIG. 84.—*Branchipus stagnalis*, ♂, in normal swimming posture (after Claus).

Long periods of frost reduce all life to a minimum: not only the cold is serious but far more so is the lack of communication with the atmosphere. Wesenberg-Lund has shown that many beetles and Hemiptera in autumn leave the smaller ponds and seek others, rich in green growth, and there live on the oxygen-supply provided by the plants under the ice for quite long periods. Only after long frost, when the plants die, these insects seek the mud and fall into a winter torpor.[6] Studies of life-cycles of the Crustacea in ponds, permanent and impermanent, are interesting and valuable (see Chapter IV, and [7, 8, 9]), and questions of dispersal of species from pond to pond, and of the association of certain species with ponds of special type (hard and soft water, etc.), are multitudinous, and always interesting.[10–15]

Each pond, however small, has its own problems: even the smallest puddles, such as lie in hollows of tree-stumps, in

old water-butts, or by the roadside, have their special interest [17] (see Chapter III, p. 68). The freshwater fauna is so varied, so pervasive, that some types, carried by wind or birds, or introduced in egg-laying, will surely find their way wherever there is water, and the study of their means of survival in unpromising situations has a fascination all its own.

The fauna of the fens and marshes in a temperate country is indistinguishable from that of the littoral zone of ponds, except for the presence of a few running-water types in dykes and lodes.[16, 18] In tropical swamps the recurrence of dry seasons conditions the predominance of types which have some method of avoiding desiccation. The abundant Rhizopod Protozoa usually encyst themselves; many swamp-Gastropods of the tropics, such as *Melania* and *Ampullaria*, close the shell-mouth with an operculum; *Spatha*, a mussel, digs its way into the mud, and many tropical fishes, *Protopterus*, *Callichthys*, and a number of small Cyprinids, also retire in this way, to reappear with startling suddenness when monsoonal rains begin to fill the watercourses once again. Air-breathing in some of these fishes, and in such types as *Ampullaria* (see p. 51), is helpful during the period of retirement and also in view of the usually low oxygen-content of the warm waters, charged with the products of decay of the abundant vegetation.

Moorland Waters

The moorland waters, in the mode of their characteristic occurrence in wide and shallow stretches and in dykes, appear not dissimilar to the marshes, but differences in the character of the substratum lead to violent contrasts in the biology of these two types. Moors are distinguished by surface-accumulations of peaty deposits formed from plant-remains, which decompose extremely slowly, forming fibrous turf which holds the water like a sponge, imparting to it an acid reaction and a brownish colour, due to "humus." Characteristic plants are *Sphagnum*, heaths, and insectivorous Phanerogams, especially *Drosera* and *Pinguicula*, in temperate climates. The presence of these last reminds us of the

PLATE XI

(*a*) A Lincolnshire fen-dyke. Dominant types among the fauna are *Limnæa stagnalis*, *Planorbis corneus*, and leafy-cased caddises.

(*b*) A Welsh moorland brook, collecting from high bogs (in the middle distance) to pass into its cascade-reach.

To face p. 216.]

poverty in nitrates, due to the slowness of organic decay and to the sponginess of the substratum.

The characteristic waters of the moors are pools, lying among the *Sphagnum*, floored with peat deposits and a surface drift of shredded plant-fragments, with brown-stained humous waters, often strongly acid in reaction. The oxygen-content is always low: at only a few centimetres' depth it may be *nil*,[19] and temperatures are astonishingly variable, often with a range as great as 32° C. during a single day.[19] The lime-content is practically *nil*.

These curious conditions constitute a severe type of biological environment. The fauna of moorland waters is mainly negative in character, distinguished by its paucity of species and the absence of whole groups. Oligochæta, Centropagidæ, Ephemeridæ, Mollusca, fishes and Amphibia—all these are usually absent, as well as many of the genera of Cladocera, such as *Moina*, *Daphnia*, and *Simocephalus*, most characteristic of ordinary ponds. Such species as occur are eurythermous: some littoral Cladocera (as *Acroperus*, *Chydorus* . . .), larvæ of dragon-flies, *Culex* and Chironomids, Cyprids (as *Candona candida*), *Stenophylax alpestris* (which makes its case of *Sphagnum*-litter), and a few *Cyclops* (especially *Cy. serrulatus*); *Holopedium gibberum* is common in some deep moorland waters.

Some few species, however, are definitely "*sphagnophile*": such are *Moraria spp.* (Harpacticidæ), *Elosa woralli* (Rotifera), *Acantholeberis curvirostris* (Cladocera), *Diphascon scoticum* (and several other Tardigrada, which cling among the tufts by their hooked claws), and some Rhizopod Protozoa, including a number of species of *Nebela*. Harnisch [19] regards the sphagnophiles as survivors of a post-glacial tundra-fauna, widespread just after the Great Ice Age, but now shrunken to special areas; the rest appear to be a "selection-fauna," composed of such immigrants from the general freshwater fauna as can endure the rigorous conditions. The peculiar rigours are oxygen-poverty, lime-scarcity, temperature-instability, acid reaction of the water *per se*, and peculiar chemical conditions. Any one of these factors may be operative in keeping out

particular species: most probably they work in combination. Certain experiments [19, 22] seem to indicate that humic acid has a definite "toxic" action which is intensified by alternations of heat and cold. Oxygen-poverty is probably serious; in rapid brooks which flow off from the moorlands the fauna increases very noticeably as the course lengthens.

The tufts of mosses growing near the edges of pools, or in hollows liable to occasional flooding, enclose a fauna of peculiar interest, adapted to make the most of such little moisture as clings between the fronds, and to endure long periods of desiccation. Rhizopoda, Rotifers, and Tardigrades, with a

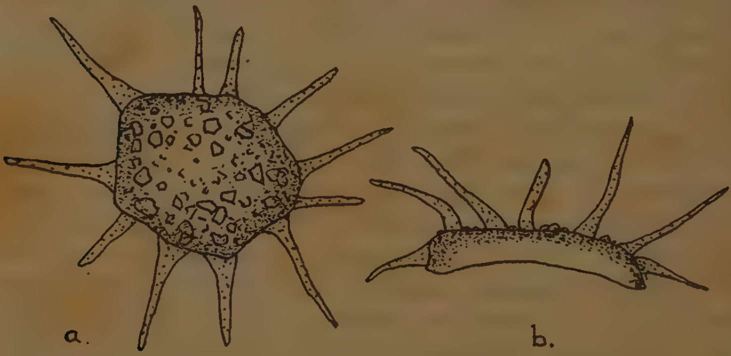

FIG. 85.—*Corycia coronata.* Variety found in moss tufts, showing chitinous spines. *a*, dorsal view; *b*, side view (after Heinis).

very few Nematode and Rhabdocœlid worms, constitute this fauna, and without exception they are distinguished by their minute size, which permits them to find shelter in the tufts. They are notoriously difficult to see: shaking the tufts in water is the best means of collecting them, but even this may fail to dislodge the great majority, for most of them have some special means of clinging to the moss. The Rhizopods cling closely by their pseudopodia, and some of them have also spinous processes from their chitinous tests, which hook among the mosses; many of the Rotifers (as *Callidina spp.*) also have spines, but for development of retention-organs of every possible sort none can compare with the Tardigrada, which are armed with hooks, claws, knobs, papillæ, and even

lash-like processes which ensure very close holding. These and the Rotifers form "resting-eggs," in drought-resistant coats, which often have a great development of spines or hooks that catch among the plants, but certain species of *Macrobiotus* shed their smooth-coated eggs into the cuticle which they cast on moulting, and this cover serves for retention.

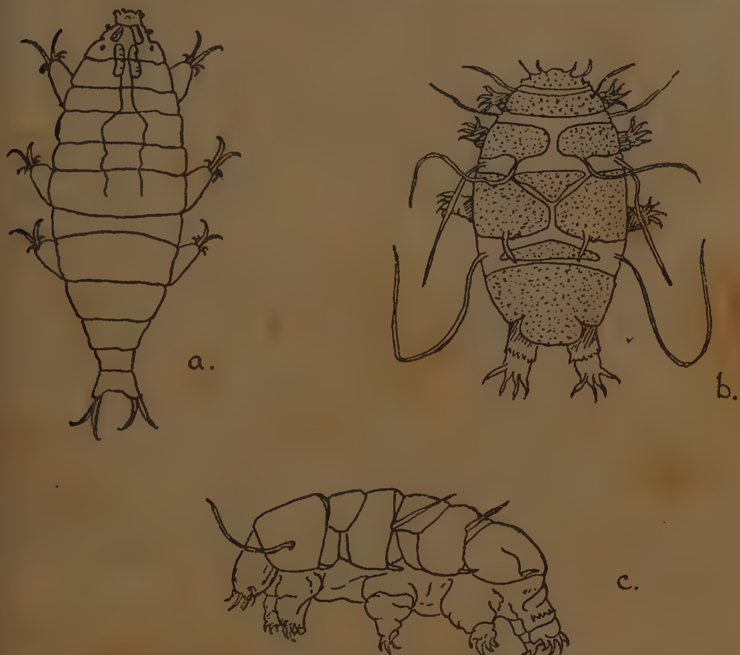

FIG. 86.—Tardigrades, showing development of hooks and other attachment-organs. *a*, *Milnesium* (after Richters); *b*, *Echiniscus* (after Richters); *c*, *Echiniscus spinulosus*, side view (after Doyère). (All magnified nearly 200 times.)

In periods of drought the worms (which lack the very special adaptations of the rest of the moss-fauna) burrow down at the roots of the sheltering plants; the Protozoa encyst; Rotifers and *Moraria* (a genus of Copepoda very common in *Sphagnum*-tufts) form resting-eggs; and Tardigrada may simply shrivel into little masses like dry sand grains, which will, however, renew their active life when water is absorbed.[23]

In some species of *Macrobiotus* a true cyst-wall is formed, and within this the whole structure of the body degenerates into a shapeless mass, with food-reserves in the form of oil-drops.[24]

FIG. 87.—*a*, Cast cuticle of *Macrobiotus tetradactylus*, with included eggs (after Greeff); *b*, free eggs of *Macrobiotus granulatus* (after Richters), showing the numerous hooklets.

Some *Callidina* (Rotifera) have been dried for thirty months, heated to 46° C. for over a week, or seven times frozen and thawed alternately, and still emerged to life after all this. *Macrobiotus oberhauseri* can endure a temperature of 100° C. for six hours at a stretch, or drying at 65° C. for as many weeks, and other species seem little less resistant. Naturally, creatures so inured to hardships and so easily distributed by wind or birds are very widespread in occurrence : nearly the whole of the moss-fauna rank as cosmopolitans, except for some few " tundra-types " which are adjudged to be most probably Ice-Age relicts.

Subterranean Waters

Our scanty information on the subject of the life of underground waters is derived from two main sources—by the arduous exploration of subterranean caverns, and by examination of material obtained from deep well-borings. From our knowledge of conditions underground, we should not expect to find the fauna numerically rich : there must be a certain scarcity of food, since home-production by the carbon-assimilation of green plants cannot take place in darkness, and food-supplies for the animals must largely consist of " wind-falls," or, more accurately, " water-borne material," trickling

in from the upper world, though this is supplemented by the subterranean fungi, and even bacteria form an item in the diet of some cave-dwellers. Further, the prevailing darkness and the constant rather low temperature of the subterranean waters (often varying little from 8° C. in European localities) make a biological environment which is highly peculiar.

The first cave-dwelling aquatic animal to be described was the famous "Olm" of Dalmatian caverns: *Proteus anguineus*, a blind newt, with eel-shaped body, unpigmented skin, and quite degenerate eyes. This find aroused great expectations of the discovery of a cavernicolous fauna structurally modified in relation to the special conditions of the habitat. The characteristics of an "ideal cavernicole," of whatever group of animals, have been defined [25] as follows:

(1) Absence of such pigments as are developed under the influence of light (certain other pigments may be produced as excretory by-products).
(2) Blindness, or reduction of organs of sight.
(3) Compensating development of tactile organs.
(4) Development of long, thin, and fragile limbs or appendages fringed with tactile hairs, *or*, if the animal lives in "cranny-waters," reduction in size and wormlike shape or flattening of the body.
(5) Absence of periodicity in reproduction, etc., owing to the constant temperature.

A number of subterranean aquatic species do pretty well conform to this ideal: especially the absence of skin-pigments and loss or degeneration of the eyes are shown in many varied types.

Proteus anguineus, a Perennibranchiate newt, has found a near relative in *Typhlomolge*, the blind white newt of the Mammoth Cavern of Kentucky, and a number of cavernicolous fishes (*e.g.* Amblyopsidæ of America) are colourless, and have degenerate eyes. There are also blind Mollusca: species of *Bythinella*, and others, and especially the *Lartetia* species of European limestone-waters. Among Crustacea Malacostraca there are a number of blind and nearly transparent forms: species of *Cambarus* and *Palæmonetes* in America, and a

Cambarus in European caves, and also *Munidopsis polymorpha*, found in the Canary Islands. Quite a number of Amphipods and Isopods conform to the type; the best-known and most common are *Niphargus puteanus* (the blind well-shrimp) and *Asellus cavaticus*. One or two blind cave-dwelling *Cyclops* species (*Cy. sensitivus*, *Cy. unisetiger* . . .), a blind Harpacticid (*Parastenocaris*), a Cyprid (*Typhlocypris eremitus*), and the peculiar *Bathynella*, further represent Crustacea among the true cavernicoles, and to these we must add a blind *Hydroporus*, a leech, *Dina absoloni*, and a Polychæte, *Troglochætus beranecki*.[26]

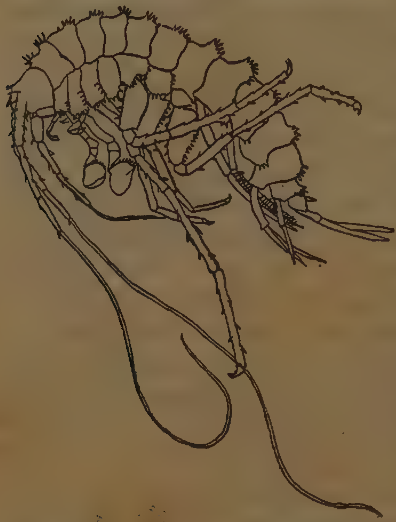

FIG. 88.—*Stygodytes balcanicus*, a blind subterranean Amphipod, with great development of "feelers" (after Absolon).

All these are blind and colourless: the larger Crustacea have the slender limbs and well-developed tactile organs which may compensate the loss of sight, while *Parastenocaris*, *Bathynella*, and *Troglochætus* all have small and very slender bodies

FIG. 89.—*Parastenocaris fontinalis* (after Schnitter and Chappuis). *a*, Female, dorsal view; *b*, male, lateral view, showing spermatophore. (Enlarged about 80 times.)

which can easily be drawn through crannies.[29, 31, 33] Undoubtedly such types as these must represent a very ancient stock of cave-dwellers. Further evidence of their antiquity,

in special cases, is not wanting: the European cave-dwelling *Cambarus* is the only species of its genus found this side of the Atlantic, evidence of its derivation from an ancient stock, while cave-dwelling Isopods of families Cirolanidæ and Sphæromidæ share with *Troglochætus*—a Polyzoan so simple in its structure as to be "almost larval" in type [33] —and with *Munidopsis polymorpha* the distinction of a close affinity with marine types.

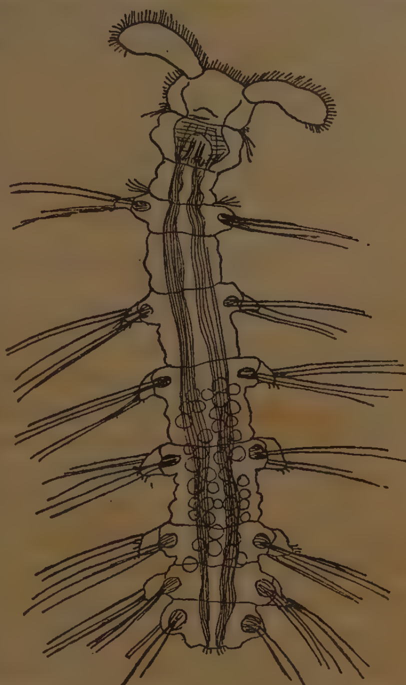

FIG. 90.—*Troglochætus Beranecki* (after Delachaux).

Whether these ancient cave-dwellers owe their blindness to their life in darkness, or whether they sought the darkness, being first blind, has formed the topic of some controversy. Among North American Amblyopsidæ some sub-aërial species are lucifuge, but have eyes, while among the subterranean species all stages in degeneration of the eyes may be observed, from one species to another [35]: probably the ancestors of most blind cave-dwellers were lucifugous, and possibly also weak-sighted.

The case of *Bathynella* must receive a separate discussion, for it has a most romantic history. So long ago as 1882 Vejdovsky found a few examples of this curious little worm-like blind Crustacean in a deep well near Prague,[27] and was puzzled to determine the affinities of the creature, which he named *Bathynella natans*. The find was very much discussed,[6] but for thirty-two years no further specimens came to hand, and biologists began to feel that *Bathynella*, like

Huxley's mythical *Bathybius*, "had not fulfilled the promise of its youth," when at last, in 1914, other specimens were found by Chappuis, in a deep well-boring near Basel. No sooner had this happened than the well fell in, and destroyed the whole site! But luck was at last in the ascendant, and within a few years another species of *Bathynella* was discovered, both in a grotto near Neuchâtel and in a shaft near Berne.[32] The new material enabled *Bathynella* to be classed with

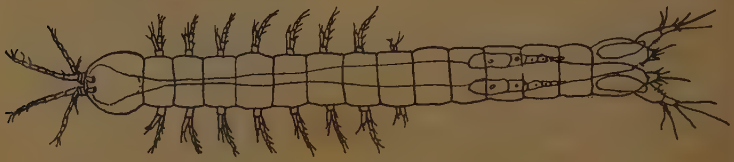

FIG. 91.—*Bathynella natans* (after Chappuis).

certainty among the Syncarida, very near to the Anaspidaceæ, whose only living representatives are found in Australia and Tasmania.[7] The case of *Bathynella* is a striking instance of the preservation of types of great antiquity in the monotonous conditions of the subterranean world.

Another set of subterranean forms, including several species of *Cyclops* and *Planaria*,[28] with very weak pigmentation, or none at all, are obviously closely related to sub-aërial types living at the present day: in one or two (e.g. *Planaria montenegrina*) the lack of pigment is the only feature distinguishing the subterranean form. These types are obviously more recent immigrants into the underground waters; Thienemann suggests that many are stenothermous species, refugees either from the increasing cold of the Ice Age or from the rising temperatures which followed it.

Still a third set of animals obtained from subterranean waters are accidental migrants, identical with above-ground species: these require no comment.

Cold Springs

The spring is the point of issue of subterranean waters to the surface; its temperature is therefore practically constant,

and differs little from that of the underground sources. Cold springs, whose average temperature is somewhere near 8° C., are most numerous in temperate regions, and most important biologically; they form the ultimate sources of many of our rivers. Springs are classified, according to their mode of egress, into three main types:

(1) *Rheocrenes*, in which the water passes through a horizontal channel, and issues suddenly, forming a waterfall, or at least a rapid stream of steep gradient, driving all finer mud aside, and leaving a clear, stony or sandy basin.

(2) *Limnocrenes*, in which the water wells up vertically into a basin lined and piled about with mud, which usually becomes richly overgrown with plants.

(3) *Helocrenes*, in which the water trickles up through a thick layer of soft earth and forms a marsh or pool about the source.

In both the last-named types the accumulation of water at the source and its admixture with mud lead to considerable changes in temperature and in solution-content. The true spring-character is best expressed in rheocrenes, and here we find the constant low temperature already mentioned, and often a high content of carbon dioxide, which imparts an acid reaction to the water, while oxygen-content is usually below saturation-values.[38] These latter features are of little consequence, as rapid flow within a few short yards adjusts the gaseous content to equilibrium with the atmosphere. Low temperature, however, *is* important.

The springs are points of contact between three regions—the subterranean, the early courses of the brooks (or ponds, in types 2 and 3), and the terrestrial proper: we find in them mingled elements from the fauna of all three.

Subterranean species often found in springs are *Niphargus puteanus* (known as the well-shrimp), *Asellus cavaticus*, blind species of *Planaria*, and *Haplotaxis gordioides*, the well-worm, which may attain a length of over a foot. Their constancy of temperature renders springs tenable by stenothermous species, and in those which lead to rapid brooks a number of the true brook-dwellers (often Ice-Age relicts), such as *Planaria alpina*,

Polycelis cornuta, species of *Rhyacophila* and other stone-loving caddises are very common; hygropetrical types also are often present.[36, 37] In limnocrenes and helocrenes the fauna, apart from subterranean species, consists of eurythermous cosmopolitans proper to ponds and marshes. The fauna of wet earth and water-margins, mentioned in Chapter VI, is well developed in springs of these two types.[37, 38, 39]

Thermal Waters

Hot springs, with temperatures constant at a level above the average of the surrounding air, occur in various regions of the earth; studies of their biology have been made especially in North America and some Italian districts.

Their peculiar features are not only constant high temperatures, but also the consequent poverty in oxygen, and the rich content of mineral matter (silica or carbonate) dissolved beneath the surface.

Their flora and fauna comprise but few species, as we might expect; what is amazing is to find that some particular species actually flourish in such situations. Green algæ have been found in calcareous springs at temperatures up to 63° C., and forms devoid of chlorophyll (especially *Beggiatoa*, sulphur-bacteria) up to 71° C., while in siliceous springs still higher temperatures may be endured.[43] Cyanophyceæ are especially resistant, and species of *Mastigocladus* and *Phormidium* most so, *Oscillatoria* next. *Mastigocladus laminosus* can endure a range of temperatures from a lower limit of 5° C. to 53° C., but seems to flourish and maintain its colour only towards the upper limit of its range[42]; some biologists believe such species to be truly "thermal"—not readapted, but direct descendants of primitive types evolved during an early phase of differentiation of the earth's surface waters—"before the oceans"—but this is speculation.

The fauna of the thermal waters is more mixed in type, and disappears at lower temperatures. The highest authenticated records are those of *Amœba limax* and some Infusoria at 50° to 52° C.; *Chironomus* larvæ at 49° C.; *Hydroscapha*

PLATE XII

(*a*) A natural rheocrene, modified by artificial treatment.

(*b*) A helocrene.

To face p. 226.]

gyrinoides at 46° C.; *Limnæa pereger* (in Iceland) at 43° C.; and species of *Laccobius*, *Bidessus*, *Hydaticus* (Coleoptera), *Philodina roseola* (Rotifera), and some Hemiptera, *Chironomus* and *Culex* at about 40° C.[40, 41, 43] The figures are astonishingly high; considering that the thermal death-point for most cold-blooded animals is between 30° and 40° C. we must infer a very considerable degree of acclimatisation to high temperatures in these species. We notice especially the predominance of air-breathing beetles and Dipteran larvæ, for whom the low dissolved oxygen-content has no terrors, and the presence of that most adaptable type, *Chironomus*.

Between 40° and 20° C. the list of species enlarges to include many of the common eurythermous types—Diptera, *Gammarus*, some *Cyclops*. . . . An Isopod, *Exosphæroma thermophilum*,[43] found in Yellowstone Park, seems to have a long thermal ancestry, since a closely related type is found fossil in Lower Oligocene hot-spring deposits; but on the whole there is probably no special "thermal fauna."

Saline Pools

In areas overlying geological formations containing rock-salt (especially Triassic strata) brine-springs and standing pools of high salinity often occur. Such waters are quite distinct from marine and brackish waters proper, not only as regards the variability of total salt-content. We have seen (Chapter II) that in sea-water there is a certain balance between the ions, resulting in a total composition favourable to the maintenance of life, but in these other saline waters the different mineral constituents (which may include chlorides, nitrates, and sulphates, mainly of sodium, potassium, and calcium) are present in varying proportions, and, whether the total osmotic concentration be to blame, or whether certain elements in excess have a "toxic" action, or both, at all events something in their constitution is inimical to many aquatic creatures.[50]

At low concentrations—up to 2½ or 3 per cent. of salts—green filamentous Algæ and *Zanichellia* (a brackish-water

Phanerogam) may still be present, together with a fauna of fairly varied character, although *Hydra*, sponges, Polyzoa, Lamellibranchs, Ephemerid and stonefly larvæ, and Amphibia are conspicuous by their absence. Above this concentration,

FIG. 92.—*Artemia salina*, the brine-shrimp (after Brauer). Actual length, about 1 cm.

species rapidly diminish in numbers, and above 10 per cent. are only found the true "halobiontic" forms,[44, 45] which rarely, or never, occur in waters other than saline.

The most famous of such creatures is the brine-shrimp,

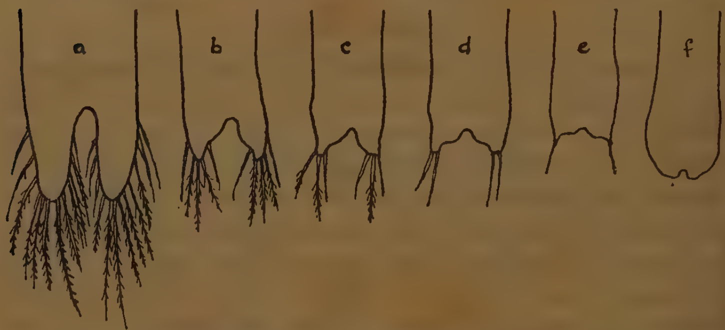

FIG. 92A.—*Artemia salina*. Lip of abdomen and caudal lobes of specimens found in localities where the salinity of the waters varied in the following relations : *a*, 8 ; *b*, 14 ; *c*, 18 ; *d*, 23·5 ; *f*, 25. (After Schmankewitsch, from Hesse.)

Artemia salina, known in saline pools from Utah (U.S.A.) to Central Asia, whose transformations in relation to salinity of the medium have been the subject of some interesting studies ([48] and Chapter I). Other halobionts are: all known species

of *Ephydra* (Diptera), and its usual parasite, *Urolepis*, *Trichocladius halophilus*, another Dipteran, *Brachionus mülleri* (Rotifera), *Nitocra simplex* (Harpacticidæ), *Dunaliella salina* (a red Flagellate), and several species of *Ochthebius*, *Philydrus*, and *Paracymus* (Coleoptera). In Westphalian pools even the

FIG. 93.—*Ephydra riparia*. *a*, Larva; *b*, pupa, about 4 times natural size (after Thienemann).

saline fauna, except *Ephydra*, dies out at 20 per cent. concentration, but in some other localities greater variety of species has been found at somewhat higher concentrations.[49] The Dead Sea is completely azoic, but rather from the presence of magnesium chlorides and bromides than from total salt-concentration, as the latter is variable from place to place, and near the coast is less than that of the water of some neighbouring springs which have a fauna of Dipteran larvæ and even small fishes (*Cyprinodon*).

A peculiar aspect of the biology of saline waters is the enormous individual development, at concentrations between 3 and 10 per cent., of a number of species, especially Dipteran, which none the less are not true halobionts, since they die out at higher concentrations, and are commonly met with in the true fresh waters. One or two species of *Cyclops*, and sticklebacks, as well as many Diptera (Chironomids, *Stratiomys* . . .), attain this " mass-development," feeding on the Diatoms, *Oscillatoria* and *Euglena*, which succeed to the filamentous Algæ of lower concentrations. These " halophiles " [45] are true freshwater species endowed with powers of resistance,[4] but the real " halobionts," which belong to the more saline waters, have their nearest kindred in the fauna of rock-pools near the sea-shore, fed by spray, and subject to great variations in salinity.[51]

The fauna of the Caspian Sea, whose high salinity is due

to long evaporation, is highly peculiar; it includes a high percentage of endemic species, some brackish water types (*Cordylophora*, *Dreissensia*), some true freshwater species (Oligochætes, Chironomids, etc.), and a seal, as well as the Crustacea *Pontoporeia* and *Chiridothea*, supposedly marine-glacial relicts. The peculiarities of the assemblage are due partly to the complicated history of the area—once a great sea basin, linked with the Black Sea—and partly to the great local variations in salinity. Near the mouth of the Volga the water is almost fresh: a bay not far away is so salt that fishes die if they stray into it, and only *Artemia salina* can survive.

Organically Polluted Waters

As every biologist knows, life is two-sided: the anabolic processes of building up complex carbon compounds have their converse in the catabolism which breaks down these unstable products into simpler bodies, with smaller molecules. When organic matter is no longer animated by life—as in excreta, or dead bodies of animals or plants—the breaking-down process continues till all its materials finally return to the environment in some form or other, but in the process the environment is robbed of free oxygen, which is restored only in combined form. This is the keynote of the striking changes produced in the life of inland water-bodies when organic waste is discharged into them in quantity.

Bacteria of putrefaction swarm in reaches polluted by organic matter, and gain their vital energy by promoting decomposition through various stages in decay, leading at last to the release of nitrates and carbon dioxide, principally. Sometimes as many as a million spores of these bacteria may be obtained from a cubic centimetre of polluted water.[52] In company with them are usually great numbers of colourless Flagellates (species of *Bodo*, and others), which feed upon the bacteria, and even on the organic waste itself, and Ciliates, especially *Vorticella* and *Paramecium*. All these may thrive on the rich food-supply, but if the pollution be at all severe it effects such a reduction in the oxygen-content of the water

that ordinary animals of larger size and all green plants totally disappear from the affected reach. A severely polluted reach is destitute of all the usual forms of aquatic life: its floor is spread with a layer of organic slime, mingled with woolly-looking masses of bacteria and detritus-feeding Protozoa, with here and there the unhealthy-looking growth of the sewage-fungus (*Leptomitus* or *Sphærotilus*); this layer is known as the "pollution-carpet."[53] Two or three Metazoa, able for special reasons to endure a scarcity of oxygen, may find a living in even seriously-polluted reaches, and, having established themselves, profit by the copious food-supply to attain to mass-development, as we have seen is the case with the few species which can endure the very similar conditions in the depths of eutrophic lakes (pp. 187–188). In the polluted reaches, just as in those, the small detritus-feeders, *Tubifex*, and *Chironomus* larvæ of the *plumosus* group, are dominant; and we notice in each case the presence of hæmoglobin in the blood. Those larvæ of *Chironomus* which have not this content always live near the surface, and in well aërated water; only the possessors of hæmoglobin can exist in conditions of extreme oxygen-scarcity, and it has been shown[54] that they are enabled to extract oxygen from water in which oxygen-tension is extremely low, below 1 per cent. of saturation. Another detritus-feeder which is equally characteristic of polluted reaches, and is even found nearer the focus of pollution than these others, is the rat-tailed maggot-larva of *Eristalis*; but it owes its resistance to quite another feature: its faculty of obtaining oxygen direct from the air, through the long "tail" (see p. 56) which encloses the air-tubes. Such resistant species, which multiply to great numbers in the polluted reaches, may be called "saprophiles," but they must be distinguished clearly from the "saprobiotic" microbes and fungi proper to polluted waters and not found elsewhere.

Passing away from the source of the pollution, recovery sets in, owing to removal of organic matter by decomposition and digestion, and absorption of oxygen from the atmosphere. In this phase, detritus-feeders are dominant: particularly

high numbers are attained by Protozoa in great variety, especially Ciliates and Flagellates, Oligochætes, and Nematodes ; to these are soon added small Lamellibranchs (especially *Sphærium*), *Limnæa*, and many Dipteran surface-breathing larvæ (as *Ptychoptera*, *Psychoda*, *Stratiomys*, Culicidæ), and

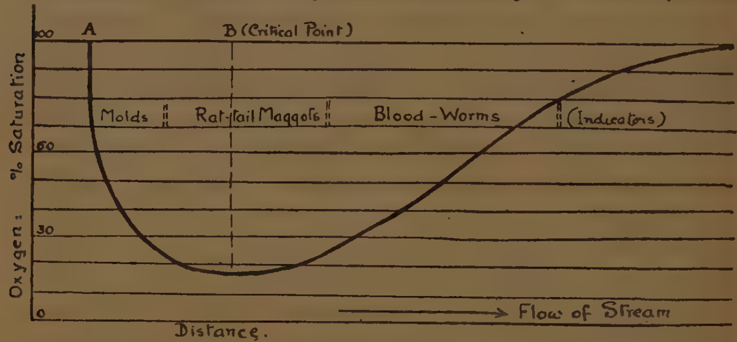

FIG. 94.—" Oxygen-sag " and biological indicators in a sewage-polluted stream (from a report of the New York State Conservation Committee).

leeches appear as soon as there is living food for them. These detritus-feeders help to clear away organic solids, and the oxygen-level is further raised by the settlement of green plants, and finally the stream attains the normal once again, but with a richer population, as its content of food-stuffs has been increased.

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CHAPTER X

THE BIOLOGY OF INLAND WATERS IN RELATION TO HUMAN LIFE

"But I remember that a wise friend of mine did usually say, 'that which is everybody's business is nobody's business.'"—IZAAK WALTON.

MAN'S outlook is incurably anthropocentric, and, without lending countenance to any theory that "the world was made for man," we cannot fail to find some interest in considering our relations with other beings which share this planet with us.

Except for fisheries, the life of inland waters does not concern us very intimately so far as economics go, although it has its own special significance none the less. Few animals of the fresh waters, other than fishes, can serve us as food. Crayfishes are esteemed a delicacy, but in this country the supply is small, and has dwindled sadly of late years, since the epoch of incidence of an epidemic disease which spread from Germany—though some say, since *Astacus fluviatilis* became a "type" in University courses! Some gastronomists appreciate the hind legs of frogs, and, judging by the evidence of kitchen-middens, the freshwater mussel was once in high favour with our ancestors in this country, but the fastidious stomach of the modern Briton mistrusts such luxuries. Freshwater mussels have another claim to our esteem: the nacreous lining of their shells can be cut into pearl buttons, and in some countries, America particularly, the sources of supply are well exploited. In Britain our water-areas, being smaller, are less productive—though perhaps this remark might be extended to cover our enterprise.

Some minor problems of control are raised by certain

pests harboured by the inland waters. Most of us have unpleasant associations with the clouds of midges, gnats, and mosquitoes that rise from stagnant water, in which they breed, and though their bites are not so dangerous here as in other countries, where they may convey the parasites of malaria and tropical fevers of various natures, yet they are sufficiently serious in many districts to constitute a pest—and every pest calls for control. The interesting study carried out at the British Mosquito Central Institute on Hayling Island, on coastal mosquitoes,[1] has shown what enterprise and skill may do towards ridding a district of a nuisance of this kind by drainage operations, while the earlier draining of the Lincolnshire Fens is undoubtedly to be thanked for the extinction of malaria as an endemic disease in these parts, where its incidence up to the seventeenth century was severe.

An evil more serious in its economic consequences is the "liver-rot" disease of sheep fed in marshy pastures. The trouble is caused by a parasite (*Distomum hepaticum*), which spends some portion of its life inside the body of a little freshwater snail, *Limnæa truncatula.* In the "cercaria" phase the parasite breaks out from the snail's body, and encysts upon damp herbage. When sheep eat these cysts the liver-flukes emerge and make their way into the bile-ducts, where they set up conditions which may lead to the death of many hundreds of sheep in a single season. Liver-rot can be treated with success medicinally, but prevention is always better than cure, and the obvious measure is to reduce the numbers of the harmless, unfortunate snail. *Limnæa truncatula* is a little creature extraordinarily hard to exterminate: being very small, and an air-breather, it requires only the least amount of moisture to keep it alive, also, it is highly eurythermous. Spraying pools on sheep-pastures with poisons, *e.g.* copper sulphate, will do a good deal, but such measures are always open to objection; draining the pastures is the better way. Even so, the most that we can hope for is reduction in the numbers of the snails, not extermination; but comparison of the incidence of liver-rot after a dry season and after a wet points the moral very clearly.[2]

Another parasite, and one which may cause trouble to human subjects in more eastern countries (not in our own), is *Bothriocephalus latus*, the broad tapeworm, which spends a part of its life in sturgeon, pike, or other freshwater fish, and transfers its attentions to such humans as take their food lightly cooked, or merely smoked. As an offset to such instances, we must mention one item on the credit side of the freshwater fauna, the use of the leech, *Hirudo medicinalis*, for purposes indicated by its name. Leech-farming was at one time quite a profitable industry, but modern science tends to pin its faith to surgery of the aseptic sort.

A certain amount of trouble is brought about in water-works by the insurgency of the aquatic population, which may multiply to such an extent on filter-beds, and even in closed pipes, as to clog them altogether. The biology of water-pipes is quite an interesting study; the conditions of high and even pressure, constant temperature, and total darkness make up an environment not unlike that to be found in the depths of lakes, but in some ways superior to it, since the constant passage of the water prevents fouling and deoxygenation, in spite of the absence of green growth, and brings a good supply of suspended food-matter. Microphagous current-feeding animals, especially such as can attach themselves to the wall of the pipe, attain enormous numbers: Polyzoa, sponges, *Hydra*, Rotifers, and stalked Ciliate Protozoa are the most important, and as there is no alternation of seasons their growth and multiplication proceed unchecked until they necessitate the cleansing of the pipe. When this is done, a remarkable collection of animals is sometimes found: eels, sticklebacks, mussels, especially *Dreissensia*, snails, worms, insect-larvæ, many small Crustacea, and even flounders have been extracted from the pipes through which a city is supplied with drinking-water.[3, 4, 5] The clogging of filter-beds is often due to Algal growth: *Anabæna*, *Oscillatoria*, and many Chlorophyceæ may cause trouble, and sometimes small Crustacea, especially *Daphnia* species. Sometimes complaints are made of the unpleasant odour or taste of drinking-water which is carefully guarded from organic pollution, and may be traced back to

the influence of Algal plankton in the reservoirs: *Uroglena* is said to impart a taste like that of codliver oil, *Anabæna*, a grassy flavour, *Synura*, an oily taste accompanied by a prickling sensation in the mouth—and so on, through a whole range of gastronomical *expertise*. A remedy of spraying reservoirs with copper-sulphate is sometimes adopted, but however carefully proportions may be calculated, the killing of the Algæ in itself renders the water temporarily very unpalatable, from their decomposition-products. A better method is that of biological control, by permitting the introduction of plankton-Crustacea, and stocking the reservoirs with fish, so killing two birds with one stone.[6]

By far the greatest economic importance of the fresh waters to us is in relation to fisheries, but, even so, the fisheries of inland waters are of relatively little significance to us in Britain, if we compare them with those of the sea. The production of edible fish in British fresh waters in 1913 was calculated to be about 2000 tons[7]: a small figure by comparison with that of 800,000 tons derived in the same year from marine fisheries. No doubt the former figure could be raised considerably, as it has certainly declined from that of former times, but it must always stand very far below the standard of marine production, as our freshwater bodies are so small. None the less, we must not look upon our gain from this source as by any means negligible, though to estimate it in terms of money-value is very difficult, as we cannot obtain complete information as to local sales. The most profitable fish obtained from our fresh waters is the salmon; though this is not a purely freshwater fish, it breeds and is caught in rivers, and thus may legitimately be considered as part of the profit we derive from them. The sales of salmon at Billingsgate, our central fish-market, amounted in 1924 (the last year for which figures are available) to about 2½ million pounds by weight of British (including Irish) fish, over 80 per cent. of the total quantity of fresh salmon sold in the British market, while in that year we exported over 600,000 lbs. to other countries.[8] The total value of the salmon sold at Billingsgate, at an average price of 1*s*. 9*d*. per lb., works out at something

like £215,000 for the year; of course, the value of all local sales should be added to this total.

There is little systematic exploitation of freshwater fishes in the narrower sense in Britain; the pollan, char, and lake-trout of some Irish and Cumberland lakes are netted for the market, also a few "coarse fishes" (Cyprinidæ) in East Anglian rivers, and eels are taken in the Norfolk Broads and elsewhere, but in all these cases neither the demand nor the supply is great. These fisheries might perhaps be made more profitable: in several countries on the Continent "coarse fish" forms an important item in the nation's bill of fare, and eel-farming and carp-farming are thriving industrial arts whose practice is based upon strict scientific principles. Carp-farming in Britain probably would not repay expenses, since the carp is of southern origin, does not feed at all in the cool season, and requires long periods of warm summer weather for its profitable growth and breeding, but eel-farming is quite another matter. Millions of elvers ascend our rivers every year in the spring "eel-fare," and they seem to flourish extremely well in shallow ponds in our country, especially on the Broads. There seems no reason why careful stocking and supervision of chosen reaches should not result in plentiful production—not multiplication, of course, since the eel is a sea-breeder, but profitable increase in growth on an economical diet of mud-living animals supplemented by judicious artificial feeding. Before the war, an enterprising German firm set up an elver-catching station in the Severn, from which the young fish were distributed to continental eel-farms, and this was subsequently taken over by our Ministry of Agriculture and Fisheries, with the idea of stimulating British enterprise. The scheme collapsed, however, for lack of support: in spite of the high nutritive value of its flesh, it seems that the eel is not in great demand as an article of diet in Britain.

No such considerations can apply to trout and salmon: the only factor which may hinder sales in their case is the high price which they fetch, owing to their comparative scarcity. Trout-farming on the European continent and in America is profitable; the spawn is obtained from "wild" females, and

fertilisation, which is, of course, external, is ensured by artificially inducing males to shed their milt, and mingling the ova and the seminal fluid in special receptacles. The hatcheries employed are usually long troughs, through which a stream of running water is kept flowing, while the escape of ova is prevented by enclosing them in loosely fitting trays of wire mesh. A series of well-irrigated pools must be maintained for later phases in development, and young fish are sold as yearlings, for planting-out in various stations. We have a few trout-hatcheries in England, but there is no commercial rearing of trout in later stages: the hatcheries supply only private owners and anglers' societies, for stocking reaches for sport.

Salmon-fishing, on the other hand, is to a large extent commercially exploited in Britain; net-fishing is carried on in the estuaries of the salmon rivers, and traps of various kinds are also used, including especially those known as "putts" and "putchers"—cone-shaped baskets, which are fixed in the estuaries, the wide mouths facing downstream, when the upward run of salmon is expected. The fish are either caught by being jammed in the small end, among the open basket-work, or retained by a trap (in "putts"). On the whole, our British rivers are probably exploited to their full present capacity (such as it is), certainly so as far as trout and salmon are concerned, between the commercial fishers and the sportsmen, and angling also for coarse fish, as pike, perch, roach, chub, dace, and so on, is the favourite recreation of quite a large section of the community. The inland fisheries of this country are subject to certain restrictions, much resembling the Game Laws, aiming at the preservation of stock from over-fishing, especially during the times of breeding; "close seasons" are defined for all food-fishes.[9] Further, no fishing, whether by rod, net, trap, or other snare, may be carried on without a licence, and the issue of licences forms quite a profitable source of revenue. The administration of all matters relating to inland fisheries is in the hands of local Boards of Conservators, endowed with powers and responsibilities for conserving the fisheries under the Salmon and

Freshwater Fisheries Acts. From their returns, we gather that the total receipts in respect of fishing from all districts south of the Tweed in 1924 amounted to over £31,000, and out of this over £24,000 was derived from personal licences issued to fishers, mainly for salmon; the income from net-fishing is thus small by comparison.[7] Net-fishing for commercial purposes employs about 2500 men in England and Wales, and, if we add to this the employment of clerks, water-bailiffs, etc., by the Fishery Boards, we see that our inland fisheries provide the means of livelihood for quite a number of people.

But let us make no denial of the fact that not in any hope of commercial profit lies our strongest interest in the life of inland waters; the deep significance which it has for us comes from the enjoyment, health, and recreation it can afford us. The pleasure which may be derived from observation of the varied life that moves and has its being within the compass of our pools and streams is not exclusively the prerogative of a few professional biologists: in our young days, we are all naturalists, and whom the gods love, and who love the world of nature, still die young, because they never can grow old. The pity is, so many of our weary citizens, not always by their own neglect, are denied refreshment at this spring of eternal youth. Some of the wisest seek it where they may; many imbibe it half unconsciously in the pursuit of some more tangible aim. Such are our sportsmen-anglers. Since the days of Izaak Walton the angler has been known for a philosopher, lured to contemplation and quiet by the rippling of the stream which spreads its lore before him like a book of pictures, whose pages turn themselves. In these days of inexpensive motor-cars and bicycles thousands of city workers find refreshment upon the banks of canals and streams from which each may sometimes take home a fish, but far more often something better still—health and a quiet mind.

But even here the unquiet city spreads its tentacles: railways stretch out along the rivers, carried on high embankments for whose maintenance the shores must be cased in cement and iron-girded; the river-bed itself must be

"rectified"—deepened in this place, straightened out in that, walled in with concrete barriers and controlled to a new course, for the furthering of traffic. The peaceful backwaters and weed-grown pools, the homes of the wild water-life, are destroyed, and the barren banks contain a sullen stream. And worse than this—down through the city run great drains and sewers, whose foul contents pour into the river, and beyond the city boundaries great factories discharge their poisonous waste along its banks. Even far away from towns, in the very heart of the ancient hills themselves, the rushing brooks run foul with mineral waste and treatment-oils and acids, and their flow is choked with heaps of stones and rubble; and everywhere the life of running waters struggles against the iron hand of industry, sometimes with patient toil repairing the waste, often succumbing, and leaving in its place foul slime and fungus-growth.

What can we do about it? Must we set the profits of industrial enterprise against the scanty gains of inland fishery, cast up the balance, and abandon the unprofitable beauty of the streams to inevitable doom? Or can we find a compromise, by which to recognise the claims of industry, and yet secure some preservation of a source of physical and spiritual profit—and monetary too, to some extent? Let us examine carefully the true facts concerning river-pollution, and try to reconstruct the stages in the degradation of our inland waters, since those palmy days when trade-apprentices had need of the protection of the law against a diet in which salmon bulked too large for tolerance.

Most of the social troubles of our day date back to the "Industrial Revolution"—the coming of the age of steel and steam. Development of the mechanical arts during the early nineteenth century led to the establishment of many factories along the banks of rivers, often for convenience of water-power. Every industrial process has its wastes, and wastes must somehow be disposed of: what could be more convenient than to dump solid or liquid refuse straight into the neighbouring stream, which might be trusted to remove such matter at least out of sight, and therefore out of mind? The

thing was done, and done universally; but this was not the worst. The working population became massed about industrial centres where machinery had been set up. Our ancestors of the day knew little of sanitation, and cared less, and in the matter of disposal of human excretory products once again the rivers were obliged to function as Heaven-provided sanitary agents. Among the poorly-housed and crowded workers diseases of epidemic character were spread and fostered by contact, atmospheric contamination, and—worse than all—the drinking of polluted water. The standard of the public health declined, and finally, in 1868, a Royal Commission was established "to inquire into the best means of preventing pollution of rivers."

This Commission obtained evidence from three main sources: municipal authorities were questioned upon their sanitation-schemes, owners of factories on the disposal of their trade-wastes, and scientists upon the possibilities of improvement schemes. Evidence from the first-named source elicited the fact that at that time most towns of reasonable size maintained a system of public sewers, along which sewage passed, for the most part entirely without treatment, even by disinfectants, directly into the nearest river or the sea. There was then no utilisation of sewage products for enrichment of the land or other purposes, and a few townships lacked a drainage system, even of this most elementary sort, entirely. Equally illuminating were replies obtained from factory owners. Except in a few cases, where solid refuse was used as road material, the whole waste was dumped untreated into the nearest body of natural water. Whatever we may say against our grandfathers, we must give them credit for an implicit trust in Providence!

The scientific evidence showed the need of more research to elaborate ideas already germinating in the minds of serious thinkers, and it is easier here to summarise the present state of knowledge upon such matters than to trace its growth from material first rendered available by the work of this Commission. It is now well known that the organic matters which bulk largely in crude sewage are composed of unstable

compounds which readily break down to simpler substances—ultimately, carbon dioxide, water, and ammonia—by oxidation, through the agency of saprophytic organisms. Under perfectly sterile conditions, this decomposition does not take place, but in nature the bacteria which further the putrefactive processes, or their spores, are everywhere present, and when sewage is discharged into a river the bacteria, and saprophytic fungi, multiply with great rapidity and carry on their work of putrefaction. The oxygen required for the new combinations is taken from the supply of this gas dissolved in the water, and if this supply be plentiful, and capable of renewal keeping place with its absorption, the work is done by the "aërobic" organisms, which only flourish in presence of free oxygen. The first stage in the process is the production of carbon dioxide, water, and ammonia from the organic waste, though a minor portion of it is used directly in the metabolism of the bacteria, from which excretory toxins are given off. In the second stage, the nitrifying bacteria come into play, and some convert the ammonia by oxidation to water and nitrous acid, a second set oxidise this latter product to nitric acid. These acids do not remain free, but combine with bases, always present, into salts, nitrites, and nitrates, which are food for plants. The whole process is hastened by the agency of microphages of various species which can ingest organic detritus. This cycle of "self-purification" in rivers is fundamental, and leads to the gradation of life below a centre of pollution which we have noticed already (Chapter IX); its ultimate outcome is the fertilisation of the stream, leading to increased plant-production, and so to a richer animal-life, which feeds the fishes—which feed man. On these lines a strong case may be made out for letting sewage run into our rivers. What need to be distressed about pollution? the river will do all the work of sanitation, and its life will thrive upon it. The answer to this question is obvious. Every river has its toleration limit, and if we overload it we shall find a very different process setting in. The ideal cycle which we have described is conditional on the presence of a sufficiency of dissolved oxygen; if this be exhausted, aërobic organisms

cease to function, and putrefaction is conducted by the bacteria of anaërobic decay. These do their work efficiently, so far as breaking down the compounds is concerned, but as an intermediate phase we get formation of poisonous ptomaine-products and evil-smelling and often harmful gases such as hydrogen sulphide and marsh-gas (methane). Under their influence the poisoned reach may extend far along the river's course, marked by the presence of these foul-smelling gases, the revolting "pollution-carpet," and the absence of normal aërobic plants and animals. In tidal rivers seriously polluted there may be formed a zone of deoxygenated and foul water, over a mile in length, which never clears, but surges up and down above the estuary with the advancing and retreating tides, and forms a permanent barrier to the entry of salmon from the sea. Such a zone occurs in the Thames near London, and in other rivers in industrial districts.

Even entirely aërobic decomposition robs the water of its oxygen, and unless the stream be swift and of good volume replacement will not equalise the matter without the formation of a zone of low oxygen-tension near the site of the pollution. This is a serious matter for the fauna, especially for fishes, and, among them, most of all for trout and salmon, which require 75 per cent. of oxygen-saturation for healthy living, at least.[10] The danger to fisheries arising from untreated sewage comes from this deoxygenation of the water, for the most part. The public health authority, while no less interested than the angler in maintaining the standard of our rivers, looks at the matter from a slightly different standpoint. What he deplores in a rough sewerage system is the production of toxic and evil-smelling substances ("a public nuisance"), and the multiplication of such organisms as the bacilli of intestinal disease, introduced with the sewage, and increasing upon the slowly decomposing matter. His aim is to hasten decomposition towards the final stages, in which the products are innocuous; and from this point of view the treatment of sewage in septic tanks, first introduced at Exeter in 1895, was once believed to be sufficient. The sewage is run into tanks, kept closed or allowed to become coated with bacterial scum,

and anaërobic decomposition there permitted to proceed. The product, if released directly to the river, is certainly damaging to fisheries, as all the oxidation processes have yet to follow; further, it has been found that, contrary to early opinion, pathogenic organisms are not destroyed by treatment in the tank, nor are the organic solids thoroughly digested, while in addition quantities of hydrogen sulphide—a thoroughly objectionable product—are generated. The use of septic tanks alone can therefore give satisfaction neither to the biologist nor to the public health authority. A modern method which gives better results includes preliminary precipitation of solids by the use of lime-digestion in septic tanks, and then aërobic treatment, by running over contact-beds of coke-clinkers, or some such material. The septic phase may even be omitted. This process may give satisfaction to the health authority, but it will not fulfil the demands of river-fisheries unless a subsequent phase of aëration, by trickling over percolating-beds, be interpolated previous to discharge into the river. Where the soil is suitable (*i.e.* not too heavy) spraying over the land may serve the double purpose of aërating the liquid and of fertilising the soil. The sewage-farm is the ultimate expression of scientific foresight and economy, provided the natural conditions be suitable. A thoroughly scientific method of sewage treatment, and one likely to satisfy all demands, because based upon sound biological principles, is that known as the "Activated Sludge Treatment": bacteria, saprophytes and microphages of various kinds play their appropriate part, concentrated within the small area of the filter-beds, and after final oxygenation a pure, harmless, and fertilising effluent is released. As a matter of fact, the system—or lack of system—of sewage-treatment in some towns and in most rural districts is still deplorable, but matters have improved considerably since the Commission of 1868.

The logical outcome of a Royal Commission is an addition to the statute-book: in this case the addition became law as the "Rivers Pollution Prevention Act" of 1876. This Act declared it an offence to put sewage or factory waste into a

stream without preliminary treatment by "the best means possible." Powers of prosecution under the Act were given only to "sanitary authorities acting under sanction of the Local Government Boards," and they were urged to "take into account the industrial interests," and "not proceed unless they are sure the industry can find means to remedy the evil without damaging its own interests." A weighty clause, this last! for it sums up the eternal dilemma: how to preserve the interests of public health and fisheries without handicapping industry. Only the scientist can resolve the problem. Regarding sewage-treatment, we have now the key to the whole solution, still, public health authorities prefer, and wisely so, to draw their drinking-water from above the sources of pollution. The last half-century has seen a great development of long-distance conduction of municipal water-supplies—witness the far-away lake reservoirs in plateau country which send down their water over a hundred miles, in some cases, to great industrial centres.

A general adoption of modern methods of sewage-treatment was accelerated by the conclusions of a second Commission on Sewage Disposal, which sat from 1898 for several years. Meanwhile the condition of our rivers as homes for fish had gone from bad to worse, and a separate Commission reported on Salmon and Freshwater Fisheries in 1902. For the first time, serious attention was paid to the effects of trade-effluents upon our fishing rivers: effluents from paper-mills, bleaching-works, wool-washings, dye-works, gas-works, tanneries, flax-steepings, breweries, coal-washings and other mining processes were all shown, on specified observations in each case, to have caused already widespread damage by their entry to the rivers. A reading to the reports of the Commission leaves one with a vision of wholesale destruction of fish-life in our finest natural rivers, with little or no attempt at restraint, although the Rivers Pollution Prevention Act had been in existence since 1872. The reasons for neglect of its enforcement were twofold: in the first place, the powers of prosecution were given only to sanitary authorities, and thus would not be used except in cases where public health was directly

concerned. Such cases were rendered fewer by the adoption of the system of long-distance water-supply, and also by an improved sewerage-treatment which yet could not satisfy the requirements of fisheries. The latter were thus left exposed to the full brunt of the pollution, without means to seek redress. The Commission led ultimately to the passing of new measures which culminated in the Consolidation Act of 1922, which tightened up the law about pollution and gave full powers of prosecution to water-bailiffs acting under Boards of Conservators, equally with sanitary officials. We have, in this standing Act, a very useful instrument for control of river-pollution, but one thing yet is seriously lacking; to understand this we must go back to the second cause of inefficiency in the working of the old Act of 1876. This Act in giving powers of prosecution, urged that they be used only in those cases where the remedy could be applied with certainty and without damage to industrial interests. This is the blank wall which still confronts us, and which the tools of science alone can demolish. The scientific advisers to the last-mentioned Commission urged the treatment of each and every class of effluent by methods found effective with regard to sewage—mainly, lime-precipitation and digestion in septic tanks—a sort of universal elixir, which promised more than it can ever fulfil.

The effluents which pour into our rivers from industrial sites are very various in their chemistry: even the contents, as regards by-products, are not yet accurately known in all cases, and even in the case of such as are known, we have no accurate conception of their influence upon the life of streams, nor of the appropriate method of remedial treatment, in the majority of cases. To take a single case, which has, by way of an exception, been worked out in considerable detail: washings from roads treated with tar-macadam bear down into the neighbouring streams solutions of coal-tar acids (phenols) which may kill trout and salmon, acting upon them as a subtle nerve-poison.[11] The poison is so insidious that very great dilution does not suffice to eliminate its action. The remedy for this evil to fisheries is to mix road-dressings

with bitumen, instead of tar—unhappily, the process is rather more expensive.

Another case in which investigation has brought to light some rather surprising facts is that of pollution from lead and zinc mines. Even when freed from all its solid matter the effluent from such works contains solutions of metallic salts which even in minute proportions only just appreciable to the chemist have a sure and deadly action on fishes. So small a proportion of the metallic base as one part in three millions is lethal in effect,[12] and to free the effluent from such content requires a special physico-chemical investigation. In other cases, still more difficult to deal with, the evidence of dead or dying fishes in the polluted reaches may be lacking: the harmful influence may affect the spawn alone, or it may even tell upon them indirectly by destroying the organisms which serve them as food. It is not enough, to proclaim an effluent harmless, to find no dying fishes in the neighbourhood: fishes are active swimmers, and quite often exhibit a repulsion from the zone of harmful influence; a better index is furnished by the general condition of the lower and less mobile organisms of the stream, especially the Mollusca. In every question of alleged pollution, the word of a biologist experienced in the study of fresh waters is the only final evidence; unfortunately the practice has been for the most part to rely entirely upon the chemist's judgment of what is likely to be harmful or innocuous: this is not enough. Biology and chemistry must work in unison to decide, first, the character of the effluent and its effect upon stream-life in various dilutions, next, the possible method of treatment, not forgetting that the treatment in itself may furnish new elements of danger. The actual concentration present in the river-water after union with the effluent may appear harmless in a laboratory test, but if a higher concentration be proved lethal, it is only right to argue the probability of ill effects from long-continued exposure to the influence of the dilute solution. Further, dilution varies according to the level of the river, and the volume of the effluent itself may at some times be greater or less. Again, an effluent harmless in the winter may be a

source of trouble in the summer, when higher temperatures intensify chemical processes and reduce the oxygen-tension. All these considerations should bear upon our judgment in cases of pollution, and each case should be judged on its own merits.

The task is immense, but till it be completed a threat of prosecution against owners responsible for polluting-effluents is a thing of farce, for they can always shelter behind the clause in the Act which binds them only to take the best means so far known to render their discharge harmless; as in the case of prosecutions lately undertaken against the owners of beet-sugar factories, whose effluents are peculiarly destructive, peculiarly difficult to treat.[13]

Meanwhile, our rivers are deteriorating: almost every day our news-sheets give us details of some fresh reach which has been devastated, and anglers, biologists, and Fishery Boards raise protests which inevitably end in a dead-lock. To organise the investigations needed, we look to the activities of a Committee fathered by three Government Departments—those of Health, Fisheries, and of Scientific and Industrial Research. Such a combination should be fertile in results, and though we know the mills of God and Government Departments ever grind slowly, we may hope that eventually they will also "grind exceeding small." In a really civilised community, with all the resources of science at its command, it should be possible to conserve prosperity without the sacrifice of so much health, beauty, and pleasure as our streams can bring us.

"Come, come, my scholar, you see the river stops our walk, and I will also stop my discourse . . . and I thank you for your patience."—Izaak Walton.

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